

A REVISION OF THE ELEPHANT-SHREWS,
FAMILY MACROSCOLIDIDAE

BY

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SYNOPSIS

Fourteen species are recognized in the family Macroscolididae. The subfamily Rhynchocyoninae contains one genus, *Rhynchocyon*, with three species. The form *melanurus* Neumann, hitherto considered a race of *R. petersi*, is believed to be a synonym of *R. cirnei macrurus*. One new subspecies of *R. cirnei* is described from southern Malawi. On the basis of an assessment involving thirty-one characters, three genera are recognized in the subfamily Macroscolidinae, *Nasilio* being considered a synonym of *Elephantulus*. *Petrodromus* and *Macroscelides* are considered to be monospecific; nine species are recognized in *Elephantulus*. Distribution maps are presented for each species, and the ecological relationships amongst the species are discussed.

INTRODUCTION

THE Macroscelididae are one of the most clearly defined groups of mammals and there has been general agreement that they are a monophyletic group not very closely related to any other group of mammals. The controversial question of their degree of affinity with the Insectivora and Primates does not therefore affect classification within the family and is not considered here. Recently strong arguments have been put forward for placing the family as the sole member of an order Macroscelidea (Butler, 1956; Patterson, 1965).

The family is confined to Africa. No comprehensive revision has previously been made and the only comprehensive list is that of Allen (1939) who grouped eighty-two named forms in forty species and six genera. Subsequently the southern African forms have been revised by Roberts (1951) and by Ellerman *et al.* (1953). The single North African species was listed, with comments on the classification of the family, by Ellerman & Morrison-Scott (1951) and the genus *Petrodromus* was revised in its entirety by Corbet & Neal (1965).

In the present study the primary object has been to delimit the species. The generic classification of the fourteen species recognized has been reviewed, and the subspecific variation described in general terms. The chance of additional species being discovered is rather slight and the specific classification can be considered to be nearly definitive, although there are one or two cases of apparently isolated pairs of forms where it is at present difficult to apply any objective criteria of conspecificity.

It is considered that formal trinominal nomenclature is frequently more misleading than useful as a method of describing subspecific variation. Subspecific names are only useful to designate completely isolated segments of a species (and only if most individuals can be recognized by their characters as belonging to one segment); or to designate contiguous segments when the zone of intergradation is so narrow as to suggest that the contiguity is secondary. In practice many forms already bearing trinomina must be considered provisionally valid until the distribution and variation are better known, but the policy has been followed of refraining from naming groups whose apparent isolation and homogeneity are probably due to absence of material from intervening areas.

The study was based on the entire collection of the British Museum, amounting to about a thousand specimens, along with smaller numbers received on loan or examined in other institutions (detailed under each species).

GENERIC CLASSIFICATION

The differences between *Rhynchocyon* (including *Rhinionax*) and the other, smaller, elephant-shrews are sufficiently numerous and great (Table 3) to leave no question about its generic distinctness, and there seems to be full justification for treating the two groups as subfamilies. Amongst the eleven species of the subfamily Macroscelidinae the genera have hitherto been based precariously on very few characters and the classification is correspondingly unstable. *Petrodromus* is the most distinct and its validity and content have never been disputed. It is characterized especially by large size and the absence of a hallux. The remaining,

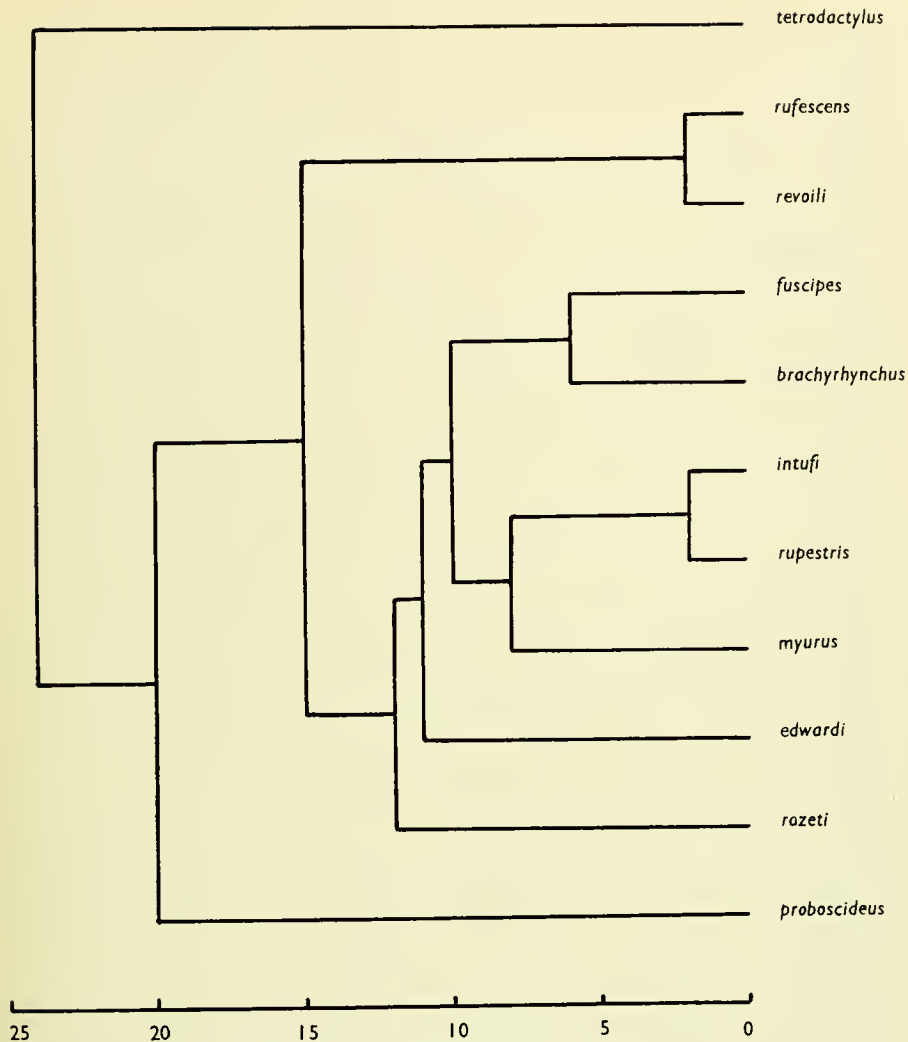
TABLE I

Specific characters in the subfamily Macroscelidinae. 2 : character fully present ;
1 : character slightly developed ; 0 : character absent.

	<i>P. tetradactylus</i>	<i>M. proboscideus</i>	<i>E. fuscipes</i>	<i>E. brachyrhynchus</i>	<i>E. rozeti</i>	<i>E. rufescens</i>	<i>E. venoili</i>	<i>E. intufi</i>	<i>E. rupestris</i>	<i>E. myurus</i>	<i>E. edwardsi</i>
Large size	2	0	0	0	0	0	0	0	0	0	0
Pelage soft and silky	0	2	0	0	1	0	0	0	0	0	0
Rhinarium hairy below	0	0	0	0	0	2	2	0	0	0	0
Pale ring round eye	2	0	1	1	0	2	2	2	1	1	1
Dark spots behind eye	2	0	0	0	0	2	2	0	0	0	0
Buff behind ears	0	0	1	2	2	2	2	2	2	1	2
Supratragus large	0	2	0	0	0	0	0	0	0	0	1
Supratragus twisted	0	0	2	0	0	0	0	0	0	0	0
Tragus large	0	2	0	0	2	0	0	0	0	0	1
Pectoral gland	1	0	2	0	0	2	2	0	0	0	0
Abdominal (third) teats	0	2	2	2	2	2	2	2	2	2	2
Hallux	0	2	2	2	2	2	2	2	2	2	2
Interdigital pads very rugose	0	2	0	0	2	0	0	0	0	0	0
Tail tufted	0	2	0	0	2	0	2	1	2	0	1
Subcaudal gland	0	2	1	2	2	2	2	2	2	2	2
Post. edge of palate highly perforate	0	2	2	2	2	2	2	2	2	2	2
Foramen between parietal and squamosal	2	2	0	0	2	2	2	2	2	2	2
Ventral elements of bullae hypertrophied	0	2	0	0	0	0	0	0	0	0	0
Mastoids grossly inflated	0	2	0	0	0	0	0	0	0	0	0
Ectotympanic part of bulla level with entotympanic part	0	0	0	0	0	0	0	0	0	2	2
Suture between premaxilla and maxilla sinuous	1	0	1	1	0	1	1	2	2	1	0
I ² : posterior cusp	0	2	1	1	1	0	0	1	1	1	1
I ³ : posterior cusp	2	2	1	1	0	0	0	1	1	1	1
I ³ : double root	2	0	0	0	1	0	0	0	0	0	0
C ¹ : double root	2	0	1	1	2	1	1	2	2	2	2
P ¹ : lingual cusp	0	0	0	0	0	0	0	2	2	0	0
P ² : anterior lingual cusp	0	2	2	2	0	1	1	2	2	1	0
P ² : posterior lingual cusp	0	2	2	2	0	2	2	2	2	2	0
P ³ : postero-external cusps as large as antero-external	0	2	2	2	1	1	1	2	2	1	0
P ₁ : double root	0	0	2	2	0	0	0	2	2	2	0
M ₃	0	0	2	2	0	0	0	0	0	0	0
Xiphisternum bifid	0	2	2	2	2	0		2		2	2
Superovulation	0*	2*		1†	0†	0†		0*	0*	2*	2*
No. of peculiar characters	4	2	1	0	0	0	0	0	0	0	0

* Data from Horst (1944).

† Observations made by Mr. H. Tripp, Zoological Society of London.



Minimum difference between members of linked groups

FIG. 1. Dendrogram showing the phenetic relationship between members of the subfamily Macroscelidinae, based on the data in Table 2. The scale is in "units of difference" as in Table 2.

overall variability. For example by including the species of *Rhynchocyon* the number of characters would immediately be increased to about seventy, but it was so obvious that thirty of these serve to separate the species of *Rhynchocyon* from

all the others (Table 3) that it was considered quite unnecessarily cumbersome to enlarge the scope of the analysis to include *Rhynchocyon*.

Table 2 shows, for each pair of species, the sum of the differences in score for each of the thirty-one characters (the maximum possible difference being sixty-two). These are presented in the form of a dendrogram in Text-fig. 1, in which the clusters have been formed by single linkage, the position of the link between two clusters representing the minimum difference between any members of the two clusters.

Considering these results at first without weighting any characters, we see that *tetradactylus* differs by never less than twenty-four units (equivalent to twelve characters) from any other species. Two other groups that show only slightly less distinctiveness are *proboscideus* by itself and *rufescens* and *revoili* together. Any division amongst the remainder would be quite arbitrary, although two other closely similar pairs are apparent within this large group, namely *rupestris* with *intufi*, and *brachyrhynchus* with *fuscipes*.

The "traditional" classification and diagnostic characters can now be considered in the light of these unweighted measures of difference. The distinctiveness of *tetradactylus* shown by the unweighted assessment is reinforced by its possession of five characters not present in any other species. These are (1) the absence of a hallux; (2) very large size; (3) the absence of four large regular perforations at the posterior edge of the bony palate; (4) the absence of abdominal mammae; and (5) the presence (but only in some areas) of knobbed bristles under the tail. In the other species the hallux, although small, is not rudimentary, and therefore its absence in *tetradactylus* can be considered a major, clear-cut difference. The knobbed bristles are only present in certain parts of the range of *tetradactylus* (and are therefore excluded from the numerical analysis), but this character is so peculiar, being apparently unknown in any other mammal, that it must be considered of some importance. This species can therefore be considered the sole species of the genus *Petrodromus*.

Of the small species, *proboscideus* is almost as distinct as *tetradactylus* and can therefore be retained as the sole member of the genus *Macrosclides*. This is reinforced by the presence of one unique, specialized feature, namely the grossly enlarged bullae. This has been treated as only two characters in the analysis but in fact it involves many parts of the auditory region that show no such enlargement in other species.

On the basis of Text-fig. 1 the pair of East African species, *rufescens* and *revoili*, form the most distinct group within the central block. However, these species have no single character that is unique to them (although the post-ocular spots are shared only by *Petrodromus tetradactylus*), they are less distinct from the group as a whole than are either *proboscideus* or *tetradactylus*, and therefore there seems no good reason to create a new genus to contain them.

The remaining seven species are interlinked by many characters and there is no justification for dividing the group on the basis of an unweighted assessment of variation. The two species that have been separated are *brachyrhynchus* and *fuscipes* (genus *Nasilio*) on the basis of an extra posterior lower molar (which is small but not rudimentary). But *brachyrhynchus* shows very close overall resem-

blance to *intufi*, differing by only five characters (Table 2) and therefore the only justification for upholding the genus *Nasilio* would be by giving overwhelming weight to this difference in dentition. The possession of third lower molars can almost certainly be considered as the retention of an ancestral character that has been lost in the other members of the family. The fact that they have been lost by such a remote relative as *Rhynchocyon* suggests that the loss of these teeth may not be a monophyletic character. There therefore seems little reason for considering this character sufficiently important to segregate *brachyrhynchus* and *fuscipes* from the remaining species with which they show many other affinities. These nine species then form the genus *Elephantulus*.

The only other grouping of species that has been made was the creation of a genus *Elephantomys* by Broom (1937) for a Pleistocene form, *langi*, along with *intufi*. This was based on a single character, the molariform P², which is in fact shared by several other species and is present in a lesser degree in yet others. Later Broom (1938) concluded that *Elephantomys* was a synonym of *Elephantulus*, not because he considered the division invalid, but because he realized that *E. rupestris*, the type species of *Elephantulus*, also belonged to the group with molariform P². He therefore considered that the group with P² sectorial should be named as a subgenus but did not in fact do so. Ellerman *et al.* (1953) gave *Elephantomys* subgeneric rank but again did not take into account those species that are intermediate in this respect, e.g. *rufescens*, *revoili*, and *myurus*. The present study supports Broom's later view that *Elephantomys* is a synonym of *Elephantulus* and rejects the validity of a subgeneric division on the basis of this character.

The fossil members of the family have recently been reviewed by Patterson (1965) who recognized eight extinct species as detailed below.

Myohyrax oswaldi Andrews, 1914 and *Protypotheroides beetzi* Stromer, 1922. These are placed in an extinct subfamily, Myohyracinae, formerly considered to be Hyracoidea. They have somewhat hypsodont molars with third molars present above and below.

Mylomygale spiersi Broom, 1946. This Pleistocene species from South Africa, represented only by an imperfect mandible, has very hypsodont molars. Broom (1948) considered it to be a very aberrant member of the Macroscelididae and Patterson (1965) agreed, placing it in a separate subfamily, Mylomygalinae. However, it is clear from Broom's account that he did not compare it with the most hypsodont of the recent species, namely *Macroscelides proboscideus*, and in fact it shows a considerable resemblance to that species, although the teeth are undoubtedly more extremely hypsodont, with a deep third lingual re-entrant angle that is not present in recent species. The overall shape of the mandible and the crowded toothrow are closely matched by *M. proboscideus*. Its separation from *Macroscelides* in a separate subfamily seems scarcely justifiable.

Rhynchocyon clarki Butler & Hopwood, 1957. A small species of *Rhynchocyon* from the Miocene of Kenya.

Metoldobotes stromeri Schlosser, 1910. A mandible from the Oligocene of Egypt, lacking M₃ and not greatly dissimilar from *Petrodromus* or *Rhynchocyon*. Placed tentatively in the Macroscelidinae by Patterson (1965).

Palaeothentoides africanus Stromer, 1932. Mandibles from the early Pleistocene of Little Namaqualand. This species has a small M_3 and appears very close to *Elephantulus brachyrhynchus* in every respect, although Patterson (1965) considered that it comes between "*Nasilio*" and *Macrosclides* and upheld its generic distinctness.

Elephantulus broomi nom. nov. We propose this name to replace *E. langi* (Broom, 1937) which name is preoccupied by *langi* Roberts, 1929, a form of *E. brachyrhynchus*. This species, from the Pleistocene of South Africa, is very close to *E. rufestris* and *E. intufi*, differing perhaps in the absence of a lingual cusp on P^1 .

Elephantulus antiquus Broom, 1948. Also from the Pleistocene of South Africa, this species appears to be very close to *E. myurus* and *E. edwardi*.

Two further fossil genera that have been allocated to the Macrosclididae (and the only ones from outside Africa) can be rejected. These are *Pseudorhynchocyon* Filhol, 1892 and *Cayluxotherium* Filhol, 1880, both from the Oligocene of France. The former has been excluded from the family by Butler & Hopwood (1957) and by Patterson (1965). *Cayluxotherium* was considered by Winge (1941) to belong to the Macrosclididae, but Butler (1948) referred it, as did Filhol, to the Erinaceidae.

These fossil species do not greatly assist in the classification of the living species. It is, however, of interest to note that species lacking the third molars were present as early as the Oligocene. The available Pleistocene species referable to, or similar to, *Elephantulus* are not sufficient to throw much light on the antiquity of the loss of third molars in this group.

To summarize the generic classification of the recent species, the eleven species of Macrosclidinae can be distributed in three genera as follows: *Petrodromus tetradactylus*; *Macrosclides proboscideus*; *Elephantulus fuscipes*, *E. brachyrhynchus*, *E. intufi*, *E. rufestris*, *E. myurus*, *E. edwardi*, *E. rozeti*, *E. rufescens*, *E. revoili*.

Family MACROSCOLIDIDAE

DIAGNOSIS. Size rather small (head and body c. 100–300 mm.); snout long, slender and flexible; ears of moderate length, reaching usually to the eye when laid forwards; fore legs rather shorter than hind; legs plantigrade or semi-digitigrade; manus with four or five digits; pes very elongate, with four or five digits; tail c. 80–120% of head and body, shortly haired; prepuce far forward on abdomen; vulva elongate; nine transverse palatal ridges; dental formula $\frac{0 \cdot 3 \cdot 1 \cdot 4 \cdot 2}{3 \cdot 1 \cdot 4 \cdot 2 \cdot 3}$; no diastema; cheek teeth forming progressive series from simple P^1 to complex molars, P^4 being largest or subequal with M^1 ; molariform teeth brachyodont or slightly hypsodont (more hypsodont in some fossil species), dilambodont; deciduous dentition well developed, not replaced until growth of body is almost complete; zygomata complete, with large jugals; auditory bullae with prominent ectotympanic, entotympanic and sphenoidal elements; lachrymals very large; sagittal crest confined to posterior half of parietals; vertebral formula 7, 13, 7, 3, c. 20–28; clavicles large; pubic symphysis long; tibia and fibula fused throughout distal half; testes dorsal; litter normally 2 or 1; caecum present.

RANGE. The Mediterranean zone of North West Africa and the whole of Africa south of the Sahara, except for the region northwest of the rivers Congo and Ubangi and west of about 27° E. (Text-fig. 18).

TABLE 3

The diagnostic characters of the two subfamilies of Macroscelididae.

	Rhynchocyoninae	Macroscelidinae
Size	Large (head and body <i>c.</i> 250 mm.)	Medium or small (head and body 200 mm. or less)
Pelage	Sparse; coarse; no long black proximal zone	Dense; fine; long black proximal zone dorsally
Mystacial vibrissae	Short, sparse	Long, abundant
Rump	Completely haired	Partly naked
Pollex	Absent	Present
Fifth digit of manus	Very short	Long
Carpal pad	Absent	Present
Proximal half of pes	Hairy below	Naked below
Mammæ	Abdominal only	Nuchal, pectoral, \pm abdominal
Post-anal gland	Present	Absent
Subterminal white zone of tail	Present	Absent
Skeleton of proboscis	Partly ossified	Wholly cartilaginous
Nasal cavity	Very wide	Narrow
Frontals	Very wide, overhanging orbits and surrounding posterior end of nasals	Narrow, scarcely overhanging orbits, not surrounding end of nasals
Anterior limit of orbit	Behind M ²	Over P ¹ /M ¹
Post-orbital processes	Present	Absent
Bony palate	Entire	Perforated
Lateral pterygoid fossae	Short and shallow	Very long and deep
Sphenoid component of bullae	Medial parts inflated	Lateral parts inflated
Paraoccipital processes	Well developed	Rudimentary
Occiput	Concave	Highly convex
Upper incisors	Absent or rudimentary	Present, functional
Upper canines	Very large	Small
Angle between ramus and coronoid process of mandible	<i>c.</i> 140°	<i>c.</i> 115°
Ulna	Thick throughout	Distal half rudimentary*
Ilio-sacral fusion	With first sacral vertebra	With first and second sacral vertebrae*
Neural spines of sacrum	Second largest	First largest*
Pubic symphysis	Not keeled	Keeled*
Uterus	Slightly bicornuate	Deeply bicornuate*
Pupil	Circular	Vertically elongate*

* Not confirmed in *E. revoili* and *E. vupestris*.

Subfamily **RHYNCHOCYONINAE**

DIAGNOSIS. See Table 3. Of the thirty characters listed in Table 3 the following seem especially important: the absence or rudimentary nature of the upper incisors; the very large upper canines; the extremely wide nasal and frontal region of the skull; the large ulna; and the more digitigrade feet, involving reduction of the lateral digits of the manus, absence of the carpal pad and the presence of hair on the proximal part of the metatarsal sole.

CONTENTS. A single genus, *Rhynchocyon*. The recognition of an additional genus, *Rhinonax*, was based on the retention or loss of rudimentary upper incisors and the difference in pattern of the pelage. The retention of upper incisors is now known to be variable within each species (Table 4).

Genus **RHYNCHOCYON**

Rhynchocyon Peters, 1847. Type-species *Rhynchocyon cirnei* Peters.

Rhinonax Thomas, 1918. Type-species *Rhynchocyon chrysoxygus* Gunther.

DIAGNOSIS. As for the subfamily (Table 3).

RANGE. See map (Text-fig. 2). Confined to forest (lowland and montane) and thick riverine bush, rarely in woodland without a closed canopy. The range appears to be limited by the Zambezi in the south, and between the Congo and Ubangi in the northwest. Elsewhere the distribution is probably limited only by habitat. The degree of fragmentation of the range is probably increasing due to deforestation.

CONTENTS. Treated here as three species which are completely allopatric with one very dubious exception, namely the possible sympatry of *R. cirnei reichardi* and *R. petersi* in the Nbuka Forest, South West Tanzania (Allen & Loveridge, 1933). This must be considered a rather provisional arrangement until the nature of the discontinuities are better known. Since they have never been kept, far less bred, successfully in captivity, the probability of directly studying reproductive compatibility is slight.

KEY TO THE SPECIES OF *RHYNCHOCYON*

- | | | |
|---|--|-----------------------|
| 1 | Rump straw-coloured, contrasting sharply with surrounding rufous pelage (Plate 1a) | <i>R. chrysoxygus</i> |
| | Rump not straw-coloured | 2 |
| 2 | Rump and posterior half of back with a pattern of dark lines or spots on a yellowish-brown or rufous ground; top of head without a rufous tinge (Plate 1d-m) | <i>R. cirnei</i> |
| - | Rump and posterior half of back black; top of head with a rufous tinge (Plate 1b-c) | <i>R. petersi</i> |

Rhynchocyon cirnei

Rhynchocyon cirnei Peters, 1847. Quelimane, Bororo district, Mozambique. Syntype examined: Leiden Museum, mounted skin, ♂.

SYNONYMY. Under subspecies.

TAXONOMIC STATUS. The inclusion of the isolated northwestern form (*stuhmanni*)

in this species is open to question, but this course is not new, having been taken by Ellerman *et al.* (1953). The form *melanurus* is here transferred from *R. petersi* to this species, since it is now known to intergrade completely with *R. c. macrurus* (but not with *R. petersi*).

DESCRIPTION (Plate 1d-m). Dorsal pelage with a pattern of three longitudinal dark lines on either side, extending from near the base of the tail forwards to about one-half or two-thirds of the distance to the ears; the central lines continuous but indented, black or chestnut; the second and third lines continuous or broken into individual spots, fainter and less extensive; the ground colour grizzled yellow or cream and black, with or without an orange-rufous wash which may almost, but never completely, obliterate the pattern; top of head grizzled cream or yellow and black.

RANGE. See Text-fig. 2. The entire range of the genus except for the coastal zones of Kenya and northern Tanzania (and Zanzibar). In southeastern Tanzania at least as far north as Kilwa (c. 8° 50' S.).

REGIONAL VARIATION. Six races can be recognized, but further collecting may well demonstrate clinal variation linking some of these or discover yet others. Of the four races that are known by specimens from a considerable number of localities two (*R. c. macrurus* and *R. c. stuhlmanni*) show internal clinal variation whilst the other two are very uniform. The overall pattern of variation cannot be assessed until more data are available from Mozambique.

R. c. cirnei

SPECIMENS EXAMINED. The type (a mounted skin, received on loan from the Leiden Museum).

DESCRIPTION. Dorsal ground colour grizzled black and yellow, becoming quite *rufous* on the rump and thighs; many contour hairs of back yellow with a dark tip but *no* grey base; dorsal spots *chestnut*, central rows reaching a little more than half-way from base of tail to ears, rather irregular, the spots of each row united by a thin medial line; second rows of spots rather faint but *discrete*; third rows just discernable; *no pale spots* between the dark ones; feet and ears as rump; ventral pelage yellowish brown, only slightly paler on throat; proximal three-quarters of tail dark brown above, paler below; distal quarter white.

RANGE. Known only from the type locality, i.e. Quelimane, north of the mouth of the Zambezi.

REMARKS. A single specimen in the British Museum from Mirrote on the Lurio River, Mozambique, i.e. much further north at 13° 50' S., 39° 35' E., has a very similar pelage, but the tail, except for the distal white zone, is totally black above and very dark brown below (Plate 1j). This specimen is in some respects intermediate between *R. c. cirnei* and *R. c. macrurus*.

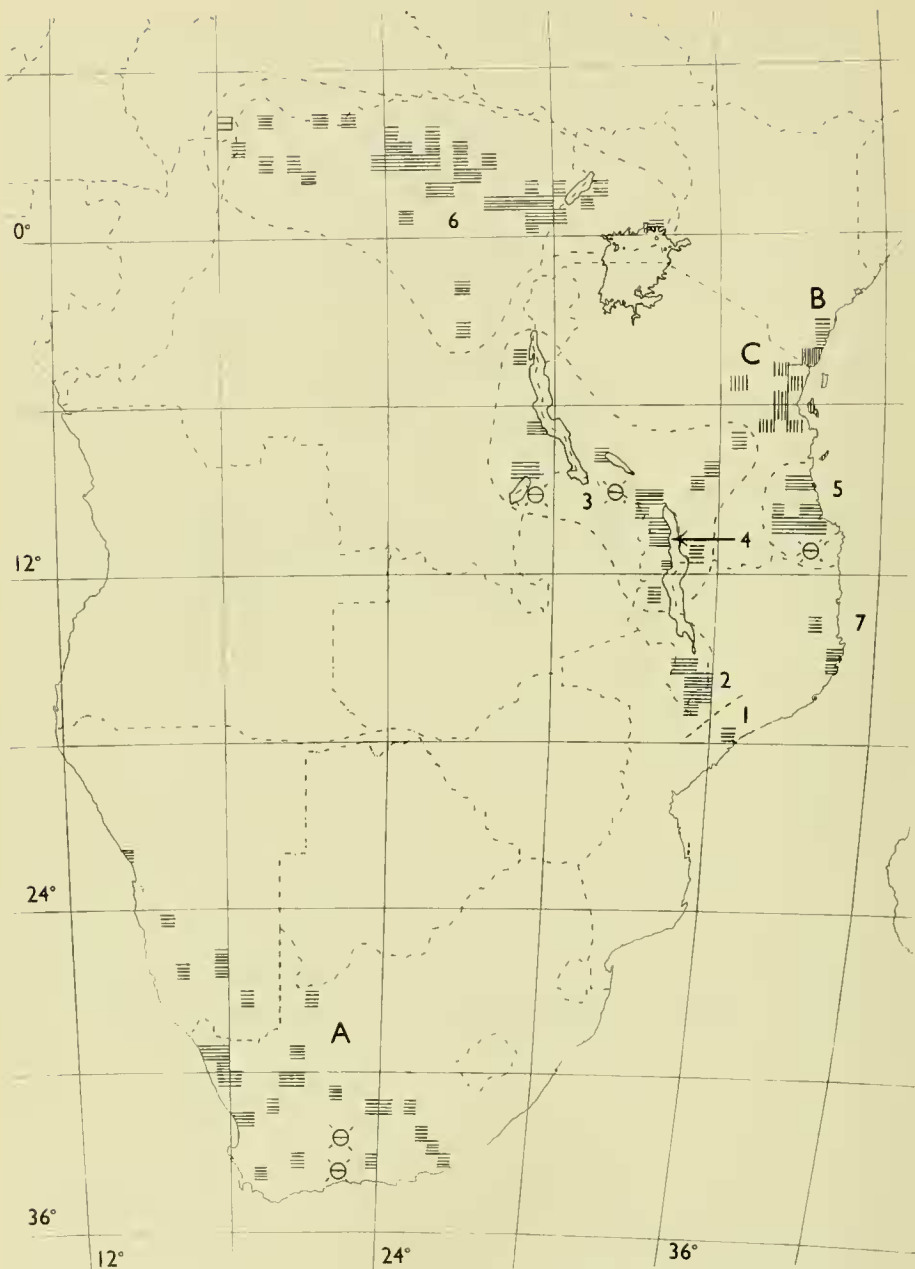


FIG. 2. Recorded distribution of A: *Macroscelides proboscideus*; B: *Rhynchocyon chrysopygus*; C: *Rhynchocyon petersi*; remainder: *Rhynchocyon cirnei*. 1: *R. c. cirnei*; 2: *R. c. shirensis*; 3: *R. c. reichardi*; 4: *R. c. hendersoni*; 5: *R. c. macrurus*; 6: *R. c. stuhlmanni*; 7: *R. c.* subsp. record unconfirmed. Circle: locality not precisely known; square: record unconfirmed.

Rhynchocyon cirnei shirensis subsp. n.

HOLOTYPE. B.M.(N.H.) number 34.1.11.8, skin, with skull, of an adult female from Lichenja Plateau, Mlanje Mountain, Malawi, 16° 00' S., 35° 33' E., altitude 1,900 m., collected by Mr. J. Vincent, 3rd January, 1932.

SPECIMENS EXAMINED. Seventeen skins and skulls from the following localities in southern Malawi: Mlanje Mt., Zomba Mt., Cholo, Chiradzulu, Chiromo, Dzonze (670–1,900 m.). The one from Dzonze was kindly shown to G.B.C. by Mr W. F. H. Ansell while he had it on loan from the Transvaal Museum; one from Mlanje was received on loan from the Leiden Museum.

DESCRIPTION (Plate 11). Dorsal ground colour grizzled black and cream, much less yellow than that of *R. c. cirnei*; contour hairs all grey-based; a very slight tinge of rufous brown on the thighs but not on the rump; pattern of dorsal spots as in *R. c. cirnei* but colour darker, a very dark blackish brown, lighter at the edge of each spot; pale spots alternating with dark ones, very slightly paler than the ground colour (including a few all-pale hairs); feet and ears slightly browner than rest of pelage; ventral pelage dull greyish buff, slightly paler on throat; proximal two-thirds of tail sharply bicoloured, the dorsal black stripe varying in width from about one-fifth to one-half the circumference; distal third white with or without a small black tip; deciduous upper canines usually with a small anterior cusp (six out of seven examined) (Text-fig. 4a and b).

VARIATION. Variation in pelage is slight. A juvenile 156 mm. long (head and body) has both the dark and light elements of the second and third rows of the pattern more distinct than the adults. One specimen from Zomba has DP³ and DP⁴ of both sides connate. The lingual aspect is normal but of the labial roots the posterior one of DP³ and the anterior one of DP⁴ are represented by a single, large root. The variation in the upper incisors is shown in Table 4.

TABLE 4
Incidence of upper incisors in *Rhynchocyon* spp.

	Animals with permanent dentition			Animals with deciduous dentition (Incisors present in all)
	Present both sides	Present one side	Absent both sides	
<i>R. cirnei shirensis</i>	7	2	2	6
<i>R. c. reichardi</i>	3	3	9	5
<i>R. c. hendersoni</i>	0	0	1	1
<i>R. c. macrurus</i>	16*	2	11	3
<i>R. c. stuhlmanni</i>	12	7	34	12
<i>R. petersi petersi</i>	5	2†	1	1
<i>R. p. adersi</i>	3	0	2	1
<i>R. chrysopygus</i>	18	1	2	1

* Two with 1/2; one with 2/2.

† One with 0/2.

RANGE. Known only from the Shire Valley of southern Malawi. The uniformity of pelage within the group suggests that the discontinuity with *R. c. cirnei* to the south and *R. c. reichardi* to the north may be real.

R. c. reichardi

Rhynchocyon reichardi Reichenow, 1886. Marungu, South East Congo. Syntype examined | Leiden Museum, skin and skull, ♀.
Rhynchocyon swynnertoni Kershaw 1923a. Kipera, Kilosa, Tanzania.

SPECIMENS EXAMINED. The female syntype (in the Leiden Museum); thirty-three skins and twenty-three skulls, from the following localities. Malawi: Nyika Plateau, Vipya Plateau, Chinteché (three from Transvaal Museum), Fort Hill; Zambia: Kayomba (Mweru Wantipa); Tanzania: Ufipa Plateau, Songea district, Kipera (type of *swynnertoni*); Congo: Fizi,¹ Mpala,¹ Lambwe² (all Tanganika district), L. Moero.²

DESCRIPTION (Plate 1h). Dorsal ground colour as in *R. c. shirensis*, grizzled black and cream, *no* rufous on rump; all contour hairs grey-based (except those of the white spots); central stripes *black* except round the edges, extending *further forwards* than in *R. c. shirensis*, to about two-thirds of the distance from tail to ears; second row of spots *confluent*, reaching as far forwards as the central pair; third rows faint but confluent and usually joining with the second to form a broad chestnut band obliterating the ground colour between the second and third rows; pale spots alternating with dark ones *white*, at least in the outer rows, least distinct in the anterior part of the central rows; feet and ears as rest of dorsal ground colour; ventral pelage paler than in *R. c. shirensis*, especially in mid-line and on the throat; proximal two-thirds of tail bicoloured, black dorsally; deciduous upper canines *lacking* an anterior cusp (twelve specimens) (Text-fig. 4c).

VARIATION. The form *swynnertoni* (only the type examined) from the north-eastern extremity shows the least development of white spots but is very closely approached in this respect by other, far distant, specimens. The southernmost locality, the Vipya Plateau (c. 12° 50' S. in Malawi), is probably also an isolated habitat and is represented by one specimen which is quite typical, showing no approach to *R. c. shirensis*. Three specimens from Chinteché (11° 50' S.) were considered by Ansell (1964) to be intermediate between *reichardi* and *cirnei* (meaning specimens from southern Malawi). These same specimens were examined by G.B.C. They are slightly deeper brown on the flanks and feet than most *reichardi* but appear very much closer to *reichardi* than to *shirensis* or *cirnei*.

RANGE. The mountains in, and flanking, the rift valley from at least 13° S. on Lake Nyasa to the northern end of Lake Tanganyika; west to Lake Mweru; much of southwestern Tanzania reaching to Kilosa in the northeast. It is probable that the extreme northeastern part of the range is fragmented.

REMARKS. Many specimens of this race have been erroneously recorded as *R. c. hendersoni* (see Ansell, 1964).

¹ In the Institut Royal des Sciences Naturelles, Brussels.

² In the Musée royal de l'Afrique Centrale, Tervuren.

R. c. hendersoni

Rhynchocyon hendersoni Thomas, 1902. Near Livingstonia, west of Lake Nyasa, Malawi.
Holotype: B.M. (N.H.) 2.9.8.1, skin, ♂.

SPECIMENS EXAMINED. The type (skin only) and two entire specimens in phenotypal from near the type locality.

DESCRIPTION (Plate 1g). Ground colour grizzled black and yellow but with the yellow subterminal bands very short, making the overall tone *very dark*, closely similar to some *R. c. stuhlmanni* from Uganda and quite different from the closely adjacent *R. c. reichardi*; pattern exactly as in *R. c. reichardi*, the resemblance enhanced by the broad, anterior part of the central black stripes and the rufous ground colour between the second and third stripes; pale spots noticeable but yellow instead of white and without pale-based hairs; proximal part of tail bi-coloured, black above; white zone subterminal and very short, beginning 40–45 mm. from tip.

RANGE. Known only from the neighbourhood of Livingstonia, Malawi. The only precise locality available is the summit of Mount Nyamkhowa (= Mt. Laws), north of Livingstonia, 2,050 m., 10° 34' S., 34° 04' E. (B.M. 36.2.20.3 and 4).

REMARKS. The presence of two other specimens virtually identical with the type confirms that this is indeed a local race and is not based on an aberrant individual as had been suspected. The close proximity of this locality to the Nyika Plateau where only *R. c. reichardi* has been collected emphasizes the highly fragmented range of this species, living in isolated patches of forest.

The name *hendersoni* has been widely and erroneously used for *R. c. reichardi* as has been pointed out and documented by Ansell (1964).

R. c. macrurus

Rhynchocyon macrurus Günther, 1881: 163. Rovuma River, east of 38° 20' E (limited by Moreau *et al.*, 1946). Holotype: B.M. (N.H.) 63.10.12.1, skin and skull.

Rhynchocyon petersi melanurus Neumann, 1900: 542. Lindi, South East Tanzania. (*Not* Uluguru Mountains: see Moreau *et al.*, 1946.)

SPECIMENS EXAMINED. The type (skin and skull); thirty-two skins and twenty-three skulls from the Liwale district, South East Tanzania (five of these in the National Museum, Nairobi); five skins and four skulls from the Lindi district (i.e. topotypical *melanurus*); ten skins and nine skulls from the Kilwa district.

DESCRIPTION (Plate 1k–m). A variable race showing a cline in the extent of a rufous wash which is minimum at Liwale (and in the type) and maximum at the coast (Lindi and Kilwa). The inland form: dorsal ground colour as in *R. c. cirnei*, much yellower than in *R. c. reichardi* and *R. c. shirensis*; rump and flanks *conspicuously rufous*, almost or quite obliterating the third row of spots; central stripes prominent, chestnut, with little or no black; second rows consisting of *isolated spots* but more prominent than in *R. c. cirnei*; pale spots absent in central rows but faintly present in second rows, creamy white; feet and ears slightly

rufous; ventral pelage rufous, except for throat and centre of chest which are pale; tail bicoloured proximally, white zone usually subterminal.

In the coastal form the rufous wash is much brighter and extends over the entire dorsal surface to just in front of the ears (but *not* the rest of the head), almost, but not quite, obliterating the pattern of stripes. These rufous hairs are all grey-based. Ventrally the rufous colour is present forward to the angle of the mouth, leaving only the inter-ramal region pale fawn. The hairs of the tail are longer and the black extends onto the ventral surface towards the end of the proximal zone.

The two extreme forms are linked by intermediates along the Mbemkuru River. At one locality (Mbemba, 10° 02' S., 38° 37' E.) two specimens have the yellow ground colour completely obliterated above, although the pattern is more conspicuous than in the coastal population; whilst one has the pattern obliterated only on the rump, with some yellow remaining between the anterior ends of the central stripes (Nat. Mus. Kenya, 4233-5). One from Mahendera, also on the Mbemkuru River (co-ordinates?), is similar to the last (B.M. 62.400-Plate 11).

RANGE. The coastal forests of Tanzania at least from Kilwa to Lindi; the Mbemkuru Valley as far as Liwale; and the Rovuma Valley.

REMARKS. The presence of these animals in the dense riverine thicket suggest that there may be a fair degree of continuity from the coast inland to Liwale, but might suggest discontinuity from one river system to another, except through the rufous coastal populations. This rufous pigmentation is, therefore, likely to be a recently acquired character in the coastal population.

This race shows rather more affinity with *R. c. cirnei* than with *R. c. reichardi* although it is clearly separable from both. The transfer of the form *melanurus* from *R. petersi* to *R. cirnei* is fully justified by the cline in variation linking the two extremes of this race and involving only a single character, namely the extent of the rufous wash. The former allocation of *melanurus* to *R. petersi* was due to a superficial resemblance, but there are in fact three quite clear-cut differences: *melanurus* lacks the pale tail, black back and rufous head of *R. petersi*.

R. c. stuhlmanni

Rhynchocyon stuhlmanni Matschie, 1893. Andunde (Bundundi), Semliki River, Congo. (See Moreau *et al.*, 1946.)

Rhynchocyon stuhlmanni nudicaudata Lydekker, 1906. Mawambi, Ituri Forest, Congo.

Rhynchocyon claudi Thomas & Wroughton, 1907a. Beritio, Uele River, Congo.

SPECIMENS EXAMINED. Five skins and skulls from Uganda; eighty-three skins, seventy-nine skulls and one entire in spirit from the Congo (most of the latter in the museums at Brussels and Tervuren, but including the types of *nudicaudata* and *claudi* in the British Museum).

DESCRIPTION (Plate I d-f). Considerable clinal variation. Ground colour grizzled black and cream or yellow, the overall colour yellowish brown in the west, very dark blackish brown in the Ituri Forest, and rather lighter greyish brown in Uganda; head concolorous with nape; central dark stripes deeply indented, anterior ends much shorter and narrower than in *R. c. reichardi*; second row dis-

jointed, short ; third row obscure but with a continuous chestnut band on the medial side as in *R. c. reichardi* ; feet very dark brown ; ventral pelage pale creamy buff in mid-line, in the darker forms limited to a narrow line (or eliminated on the thorax) by encroachment of the dorsal colour ; tail either completely pallid (in west) or with the proximal two-thirds pale brown above, *never black* ; white zone very variable, usually detectable and usually subterminal ; *nasals short* (extension behind maxillae less than 13% of condylobasal length).

RANGE. The lowland rain forest of the Congo between the rivers Congo and Ubangi, south at least to 3° 10' S., north to the River Uele (both banks) and east to the foot of the volcanic highlands of Kivu ; also isolated populations in at least four areas of lowland forest in Uganda, namely Bwamba, Bugoma, Budongo and Mabira. A single juvenile in Paris Museum is reputed to have been collected in 1966 between Bangui and M'Baiki, Central African Republic, i.e. on the right bank of the Ubangi River.

VARIATION. The ground colour shows a cline from yellowish brown in the west, with which the pattern contrasts clearly, to very dark brown in Ituri where the pattern may be almost completely obscured. The western form differs clearly from *R. c. reichardi* in the yellow-brown wash, especially on the shoulders and neck, and in the all-white tail. The Uganda specimens have the base of the tail more clearly bicoloured. Although the pattern is obscure the pale spots are always visible. Too few specimens are available from the Uganda forests to show whether there are any constant differences between these widely isolated populations. The two specimens available from the Budongo Forest have the throat yellowish buff, darker than at all the other eastern localities. The deciduous upper canine has an anterior cusp in six out of sixteen skulls. The single specimen reputedly from the Central African Republic is indistinguishable from specimens from the western part of the range in the Congo.

REMARKS. Of all the races of *R. cirnei* this one is the most distinct and could with some justification be treated as a species. The short nasals distinguish it, although with a slight overlap, from the other two species of *Rhynchocyon* as well as from the other races of *R. cirnei*.

Rhynchocyon petersi

Rhynchocyon petersi Bocage, 1880. Mainland opposite Zanzibar (see Dollman, 1912).

SYNONYMY. Under subspecies.

TAXONOMIC STATUS. This species appears to continue the clinal variation shown within *R. cirnei macrurus*. However, the major discontinuity (geographical and morphological) is between *petersi* and "*melanurus*", not between "*melanurus*" and *macrurus* as suggested by the current classification. Further collecting in the area between Kilwa and the Uluguru Mountains may serve to confirm or reject the specific separation of *cirnei* and *petersi*. On the other hand it is possible that extinction, perhaps recent due to deforestation, may have destroyed the evidence.

DESCRIPTION (Plate 1b-c). Rump and centre of back black (extending forwards almost to scapular region); rest of upper surface and flanks orange-rufous or dull maroon without grey bases to the hairs; head tinged with rufous but somewhat grizzled; pattern of *R. cirnei* obliterated except that the central dark stripes can be seen with difficulty in good light; ventral pelage, including whole of throat, orange-rufous or maroon; feet and ears orange-brown; tail very pale orange-brown, the long black hairs of the rump extending onto the tail in the form of a wedge; subterminal white zone usually visible but obscure.

RANGE (Text-fig. 2). Forests of the coastal region of Tanzania and Kenya from at least 6° 45' S. (near Dar-es-Salaam) to the Rabai Hills, Kenya (4° 00' S.); the islands of Zanzibar and Mafia. The westernmost locality is Kibaya (Swynnerton & Hayman, 1951). This is far into the steppe zone and is presumably an isolated forest habitat.

Allen & Loveridge (1933) accepted a sight record of this species made by Loveridge's local assistant in the Nkuka Forest, Rungwe Mountains, where a series of *R. cirnei reichardi* was obtained (erroneously reported as *R. c. hendersoni*). This seems so unlikely that it cannot be accepted (nor rejected) without confirmation. There is also the possibility that it was an abnormal rufous individual of *R. cirnei* similar to the coastal form of *R. c. macrurus* (i.e. "*R. petersi melanurus*") rather than a true black-backed *R. petersi*.

VARIATION. Two subspecies can be recognized, the form on the islands being distinct from that on the mainland. There is no clinal variation within the mainland race showing any approach to either *R. cirnei* or to *R. chrysofygus*.

R. p. petersi

Rhynchocyon petersi usambarae Neumann, 1900: 542. Usambara, Tanzania.

Rhynchocyon petersi fischeri Neumann, 1900: 543. Uzigua, Tanzania: "between 5° 20' and 5° 30' S, 37° 50' and 38° 40' E." (Moreau *et al.*, 1946.)

SPECIMENS EXAMINED. Thirteen skins, ten skulls and one entire from the following localities. Tanzania: Makindo, Mandera, Vihinga, Amani; Kenya: Shimba Hills, Rabai Hills. Of these one skin and skull were in the National Museum, Kenya, and four skins and five skulls were in the Paris Museum.

DESCRIPTION (Plate 1b). Pelage of shoulders, flanks and ventral surface *orange-rufous*, head showing more yellow; feet orange-brown, lacking black-zoned hairs; tail very pale orange at base becoming cream-coloured distally, white subterminal zone faintly or not visible.

RANGE. The mainland part of the species' range.

REMARKS. There is a gap of about 200 km. between the nearest known localities of *R. c. macrurus* and this race, and of about 30 km. between *petersi* and *chrysofygus* to the north. But there is no hint of clinal variation *within* this race tending towards either of these neighbouring species. Moreover, in each case the difference involves several characters. Neumann's form *usambarae* was distinguished by the absence of a white zone on the tail (compared with specimens from Zanzibar Island,

not *R. p. petersi*). The distinctness of the white zone is variable, even at one locality, e.g. the Shimba Hills, and therefore cannot be used to validate a race *usambarae*. An approximately topotypical specimen of *usambarae* from Amani has been examined in the National Museum, Nairobi. Newmann's *fischeri* was based on a specimen with the underparts pale, but this again was in comparison with material from Zanzibar (*R. p. adersi*). No topotypical specimens have been examined but it seems unlikely that this name is valid.

R. p. adersi

Rhynchocyon adersi Dollman, 1912. Zanzibar Island. Holotype: B.M. (N.H.) 12.1.6.1, skin and skull.

SPECIMENS EXAMINED. Six skins and five skulls (including the type) from Zanzibar Island; one skin and skull from Mafia Island.

DESCRIPTION (Plate 1c). Pelage of shoulders, flanks and ventral surface *dull maroon*, head paler but rufous rather than yellow; feet dark reddish-brown, the hind feet especially with many black-banded hairs; tail brighter orange-brown than that of *R. p. petersi*, contrasting more sharply with the white zone which is usually terminal.

RANGE. Zanzibar and Mafia Islands.

Rhynchocyon chrysopygus

Rhynchocyon chrysopygus Günther, 1881:164. "River Mombaça", corrected by Moreau *et al.* (1946) to "Mombasa, Kenya Colony". This must be interpreted rather vaguely as Mombasa district, since there is no evidence of the presence of this form closer to Mombasa than Takaunga, 40 km. to the north. Lectotype (Thomas, 1918): B.M. (N.H.) 80.11.30.7, skin and skull.

SPECIMENS EXAMINED. Twenty-nine skins and twenty-two skulls, including the type, from the following localities in Kenya (neglecting the type locality): Takaunga; Sokoke Forest; Arbagundi, Galana River; Gede; Malindi. Of these twenty-one skins and seventeen skulls are in the National Museum, Kenya.

DESCRIPTION (Plate 1a). Pelage of flanks, thighs and back (except rump and head) maroon, similar to that of *R. petersi adersi* but with an admixture of black hairs; rump straw-coloured; central dark stripes of the *R. cirnei* pattern represented by black anterior parts (on maroon ground) and by two rufous marks near the anterior edge of the straw patch, but absent from the posterior part of the rump; second rows faint but visible, third rows obscure; pale spots of the *R. c. reichardi* pattern faintly visible in the second rows, more obscurely in the central rows; top of head grizzled cream, brown and black, closer to *R. cirnei* than to *R. petersi*; ventral pelage only a little paler than dorsal except on throat; feet and ears almost black; proximal part of tail bicoloured, black above, shortly haired except for a tuft of long black hair about 50 mm. from the root; white zone long and subterminal.

VARIATION. Pelage very constant, but one animal shows partial albinism, having white on the nape, in front of the ears and slightly on the flanks.

RANGE. The coastal forests of Kenya from at least 3° 40' S. north to the Galana River (Text-fig. 2).

REMARKS. Without knowing what form of *Rhynchocyon*, if any, occurs in the small area between the known ranges of *R. petersi* and *R. chrysopygus*, three alternative situations can be postulated: (1) there is a continuous population with a cline linking the two forms (indicating conspecificity); (2) there is a continuous population with an abrupt boundary (indicating a *specific* difference); or (3) there are no representatives of the genus in the intervening area. The absence of clinal variation *within* either of the known forms makes the first alternative unlikely. The last alternative seems the most probable but one must postulate an isolation of rather long standing to account for the very considerable differences involved.

Subfamily MACROSCOLIDINAE

DIAGNOSIS. See Table 3.

CONTENTS. Three genera, two monospecific, the other with nine species.

RANGE. That of the family except for the lowland rain forest of the Congo north of the Congo River.

KEY TO THE GENERA OF MACROSCOLIDINAE

- 1 Hallux absent; size large (head and body of adult over 160 mm., condylobasal length over 45 mm., upper tooth-row over 25 mm.); two pairs of mammae (antebrachial and pectoral) **PETRODROMUS**
- Hallux present; size smaller (head and body under 160 mm., condylobasal length under 40 mm., upper tooth-row under 22 mm.); three pairs of mammae (including abdominal) 2
- 2 Auditory bullae grossly inflated (Text-fig. 6a) (they can be felt through the skin as a pair of prominent swellings on the *dorsal* surface of the skull on either side of the occiput); teeth very crowded, posterior ones rather hypsodont (Text-fig. 9a) **MACROSCOLIDES**
- Auditory bullae not grossly inflated (Text-fig. 6b and c); teeth less crowded and less hypsodont (Text-fig. 9b-j) **ELEPHANTULUS**

Genus **PETRODROMUS**

Petrodromus Peters, 1846. Type-species *Petrodromus tetradactylus* Peters.

Cercoctenus Hollister, 1916. Type-species *Petrodromus sultan* Thomas.

Mesocctenus Thomas, 1918. Type-species *Petrodromus rovumae* Thomas.

DIAGNOSIS. Hallux absent; size large (head and body of adult over 160 mm.); two pairs of mammae; palate relatively entire, lacking very large perforations between M¹-M¹; I¹ prominent, more than twice as long as I²; I³ double-rooted.

CONTENTS. A single, variable species, with one or two marginal forms that may prove to justify specific rank.

Petrodromus tetradactylus

Petrodromus tetradactylus Peters, 1846. Tette, Mozambique.

SYNONYMY. Under subspecies.

TAXONOMIC STATUS. The form *tordayi* (Congo), here included in this species, could with some justification be treated as a distinct allopatric species. The other races are either very little differentiated, or highly differentiated but connected by extensive intergradation.

DESCRIPTION. See diagnosis of genus above, and the characters listed in Table 1.

RANGE. See map (Text-fig. 3). Forest, thicket and the denser types of savanna woodland from Natal north to the Galana River in Kenya, and northwest to the Congo River.

REGIONAL VARIATION. Extensive and complex. It has been described and discussed in detail by Corbet & Neal (1965) and only an outline is presented here. The range is much more continuous than that of *Rhynchocyon* spp. and some of the races listed below must be considered provisional since it is probable that further collecting will confirm the widespread existence of clinal variation.

P. t. tetradactylus

Petrodromus matschiei Neumann, 1900 : 541. Barungi, Tanzania (c. 5° 10' S., 36° 00' E. according to Moreau *et al.*, 1946).

Petrodromus venustus Thomas, 1903. Namwiwe, Zambia, c. 10° 05' S., 33° 20' E., according to Ansell *et al.* (1962).

Petrodromus occidentalis Roberts, 1913 : 69. "Northwestern Rhodesia".

Petrodromus robustus Thomas, 1918 : 367. Upper Lufua River, Katanga, Congo.

DESCRIPTION. A variable race. Dorsal pelage without a clearly defined central stripe ; ventral pelage white ; mid-ventral hairs of the tail unspecialized or with a few slightly enlarged ; sutures between premaxillae and maxillae sinuous ; posterior palatal vacuities large (Text-fig. 5a).

VARIATION. There is a cline from southeast to northwest across Zambia, the northwestern form "*robustus*" being very large with almost no buff on the flanks.

RANGE. From the Zambezi through Zambia and Malawi to Katanga, and through western Tanzania as far as Ruanda and Kondoia.

P. t. rovumae

Petrodromus rovumae Thomas, 1897 : 434. Rovuma River, 100 miles inland. Holotype : B.M. (N.H.) 63.10.12.2, in phenoxytol with skull extracted, ♀.

Petrodromus nigriseta Neumann, 1900 : 541. (Nomen nudum).

Petrodromus (Mesoclenus) mossambicus Thomas, 1918 : 369. Cabaceira, Mozambique.

DESCRIPTION. Dorsal pelage without a clearly defined dorsal stripe ; ventral pelage usually white, occasionally tinged buff ; mid-ventral hairs of tail usually large and club-shaped, occasionally with a terminal knob ; sutures between premaxillae and maxillae sinuous ; posterior palatal vacuities usually small (Text-fig. 5b).

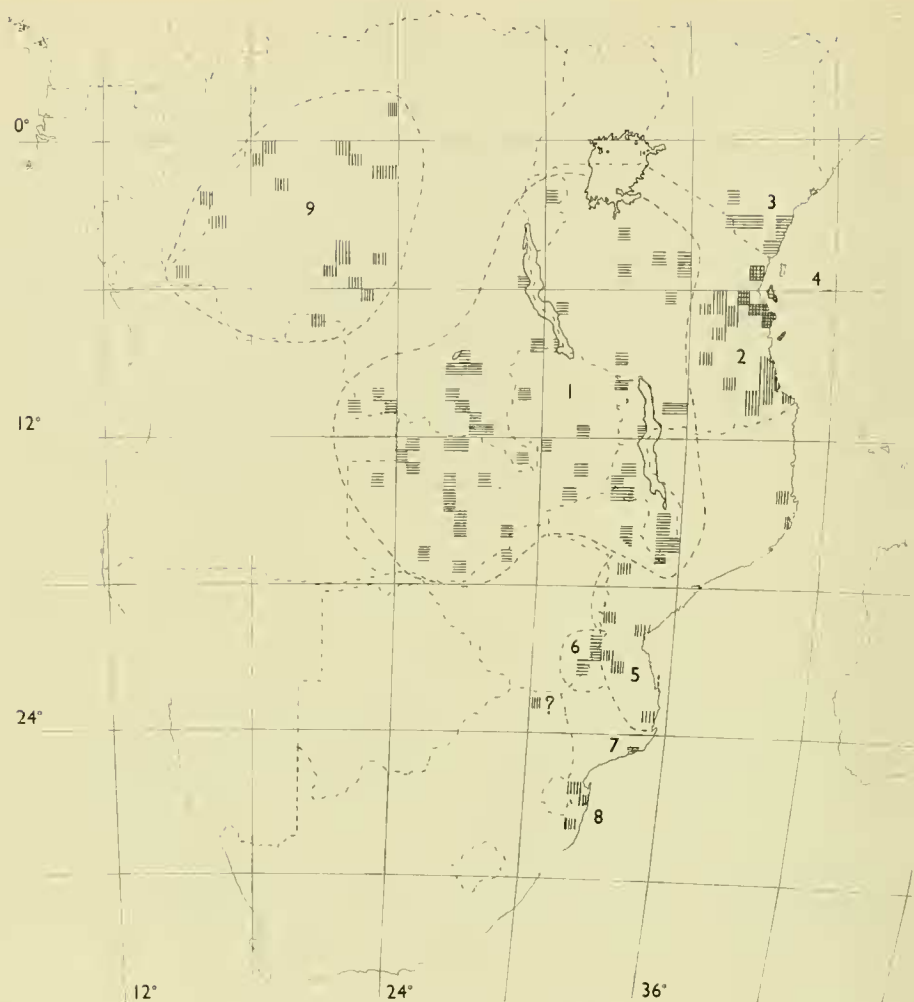


FIG. 3. Recorded distribution of *Petrodromus tetradactylus*. 1: *P. t. tetradactylus*; 2: *P. t. rovumae*; 3: *P. t. sultan* (incl. *sangi*); 4: *P. t. zanzibaricus*; 5: *P. t. beirae*; 6: *P. t. swynnertoni*; 7: *P. t. schwanni*; 8: *P. t. warreni*; 9: *P. t. tordayi*.

VARIATION. There is very great individual variation in the mid-ventral bristles of the tail. The southern form "*mossambicus*" tends towards *P. t. tetradactylus* in that the caudal bristles are less developed and the palatal vacuities are rather larger (not smaller as stated by Thomas (1918)). The complex variation in north-eastern Tanzania is described below under *P. t. sultan*.

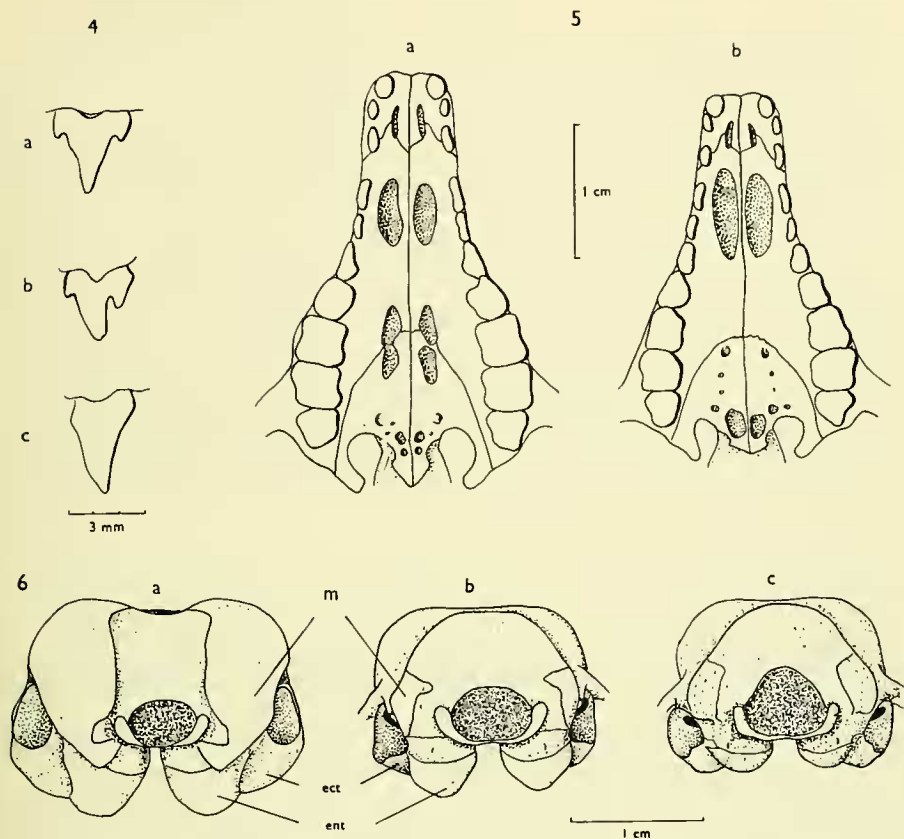


FIG. 4. Left DC¹ of *Rhynchocyon cirnei*. (a) *R. c. shirensis* (B.M. 11.7.3.1); (b) ditto (B.M. 10.9.21.1); (c) *R. c. reichardi* (B.M. 11.1.29.4). Anterior edge to the left.

FIG. 5. Palate of *Petrodromus tetradactylus*. (a) *P. t. tetradactylus*, South West Tanzania (B.M. 33.8.19.1); (b) *P. t. rovumae*, eastern Tanzania (B.M. 22.7.17.105).

FIG. 6. Occipital views of skull. (a) *Macroscelides proboscideus* (B.M. 4.2.3.12); (b) *Elephantulus rupestris* (B.M. 25.1.2.33); (c) *Elephantulus myurus* (B.M. 1.7.9.5). *ect*: ectotympanic component of bulla; *ent*: entotympanic component of bulla; *m*: mastoid.

RANGE. Eastern Tanzania and northeastern Mozambique.

REMARKS. This race may prove to intergrade with *P. t. tetradactylus* in the south (in Mozambique), but there is no indication of intergradation with the typical race in western Tanzania, from which *P. t. rovumae* can be distinguished by the knobbed bristles and relatively entire palate (Text-fig. 5).

P. t. sultan

Petrodromus sultani Thomas, 1897: 435 (corrected to *sultan* by Thomas (1898)). Mombasa, Kenya. Holotype: B.M. (N.H.) 80.11.30.10, skin and skull, ♂.

DESCRIPTION. Dorsal pelage with median reddish brown zone narrow and discrete, flanked by zones of pure grey; mid ventral bristles of tail very long, and expanded at the tip to form a clearly defined knob, tail almost naked above; ventral pelage usually buff; skull large (upper tooth row over 28 mm.); rostrum narrow; sutures between premaxillae and maxillae not sinuous; posterior palatal vacuities absent or almost so; nasals short (less than 130% of frontals).

VARIATION. Very slight except in the region of contact with *P. t. rovumae* (see below).

RANGE. The coastal area of Kenya and Tanzania from the Galana River south to the Pangani River, with a zone of hybridization with *P. t. rovumae* extending further south at least to Dar-es-Salaam.

REMARKS. In the region where this race overlaps with *P. t. rovumae* animals occur with all combinations of "rovumae" and "sultan" characters—there is no cline with uniformly intermediate characters.

P. t. sangi

Petrodromus sultani sangi Heller, 1912. Mount Mbololo, Taita Hills, Kenya. Holotype: U.S. Nat. Mus. 181822, ♂.

DESCRIPTION. Differs from *P. t. sultan* only by the pale, rather yellowish, colour of the dorsal stripe.

RANGE. Only known from the type locality. This may be an isolated population; a specimen from Taveta is typical of *P. t. sultan*.

P. t. zanzibaricus

Petrodromus tetradactylus zanzibaricus Corbet & Neal, 1965. Makunduchi, Zanzibar Island. Holotype: B.M. (N.H.) 19.6.9.10, skin and skull, ♀.

DESCRIPTION. Dorsal pelage with the central zone discrete and separated from the buffy flanks by zones of pure grey, as in *P. t. sultan*, but rather less red; caudal bristles knobbed; smaller than *P. t. sultan* (upper tooth-row under 28 mm.); rostrum relatively wide, tooth-rows convergent anteriorly as in *P. t. rovumae*; sutures between premaxillae and maxillae sinuous as in *P. t. rovumae*.

RANGE. Zanzibar Island.

REMARKS. This is a fairly uniform population showing a mixture of the characters of *sultan* and *rovumae*.

P. t. beirae

Petrodromus beirae Roberts, 1913: 69. Zimbiti, Beira, Mozambique. Holotype: Transvaal Museum, skin and skull, ad. ♂.

DESCRIPTION. Dorsal stripe diffuse; flanks bright buff, sharply demarcated from the white ventral pelage; tail lacking specialized bristles and almost naked above; skull as in *P. t. tetradactylus* but P^3 commonly with an anterior cusp.

RANGE. Known from the Beira and Gorongozo districts of Mozambique, i.e. south of the Zambezi, and from the south bank of the Save River (Dalquest, 1965).

P. t. swynnertoni

Petrodromus tetradactylus swynnertoni Thomas, 1918: 368. Chirinda Forest, Melsetter, Rhodesia. Holotype: B.M. (N.H.) 8.7.19.10, skin and skull, ♂.

DESCRIPTION. Dorsal pelage duller than that of *P. t. beirae* and the nominate race; tail thinly haired above so that the scales are obscured.

RANGE. Montane forest of the Melsetter district, Rhodesia.

REMARKS. This form is doubtfully distinguishable from the nominate race but may prove to intergrade with *P. t. beirae*.

P. t. schwanni

Petrodromus schwanni Thomas & Wroughton, 1907b. Coguno, Inhambane, Mozambique. Holotype: B.M. (N.H.) 6.11.8.32, skin and skull, ♂.

DESCRIPTION. Dorsal stripe diffuse but rather grey; flanks grey, with very little buff, not sharply demarcated from belly; ventral pelage usually buff; caudal bristles knobbed as in *P. t. sultan*; skull as in *P. t. tetradactylus* except that the posterior palatal vacuities are small or absent, as in *P. t. sultan*.

RANGE. Known only from the type locality. Corbet & Neal (1965) postulated that this form might be isolated between the Limpopo and Save Rivers, but Dalquest (1965) has since recorded *P. t. beirae* from the Save river and has confirmed (*in litt.*) that his specimens did indeed lack knobbed bristles and did come from the south side of the river.

REMARKS. This race resembles *P. t. sultan* in two characters, the knobbed caudal bristles and the entire palate, but more closely resembles the nominate race in all other respects.

P. t. warreni

Petrodromus tetradactylus warreni Thomas, 1918: 364. Mangazi, Zululand, Natal. Holotype: B.M. (N.H.) 18.4.9.1, skin and skull, ♂.

DESCRIPTION (based only on the type). Similar to the nominate race but flanks grey with very little buff; tail very scantily haired, ventral hairs normal.

RANGE. Coastal region of northern Natal and adjacent part of Mozambique.

P. t. tordayi

Petrodromus tordayi Thomas, 1910. Misnmba, Sankuru River, Congo. Holotype: B.M. (N.H.) 9.12.12.5, skin and skull.

Petrodromus tordayi tumbanus Kershaw, 1923b. Bikoro, Lake Tumba, Congo.

DESCRIPTION. Dorsal pelage darker than in any other race, not forming a discrete stripe; buff stripe on flanks very prominent; ventral pelage cream, often washed with buff; tail nearly naked; size considerably smaller than in the adjacent Katangan form of *P. t. tetradactylus* (condylo-basal length usually under 50 mm.); skull as in the nominate race.

VARIATION. The ventral pelage is variable and in some individuals the orange-buff of the flanks extends over the entire under-parts without interruption.

REMARKS. There is an apparent gap between the range of this race and the very large form of the nominate race in Katanga. The morphological differences are sufficiently sharp and numerous to suggest that there is no intergradation between the two forms. This must be considered a potential species, although there is no character that distinguishes it from *all* other races.

Genus **MACROSCELIDES**

Macroscelides Smith, 1829 Type-species *M. typus* Smith = *Sorex proboscideus* Shaw.

Eumerus I. Geoffroy, 1829.

Macroscelis Fischer, 1830.

Rhinomys Lichtenstein, 1831. Type-species *R. jaculus* Lichtenstein = *Sorex proboscideus* Shaw.

DIAGNOSIS. Auditory bullae enormously enlarged, involving the mastoids and parts of the occipital, squamosal and parietal bones; two lower molars; posterior teeth rather hypsodont; hallux present; three pairs of mammae (antebrachial, pectoral and abdominal).

CONTENTS. A single species.

REMARKS. The osteological description of this genus by Evans (1942) is invalid since he mistakenly used *Elephantulus rozeti* to represent the genus *Macroscelides* in contrast to *E. rufescens* representing *Elephantulus*.

Macroscelides proboscideus

Sorex proboscideus Shaw, 1800: 536. "Cape of Good Hope", limited by Roberts (1951) to Roodeval, Ondtshoorn division, southwestern Cape Province.

Macroscelides typus Smith, 1829. "Interior of South Africa".

Rhinomys jaculus Lichtenstein, 1831. "East coast of South Africa".

Macroscelides typicus Smith, 1838.

Macroscelides melanotis Ogilby, 1838: 5. Between Cape Town and Damaraland.

Macroscelides proboscideus hewetti Roberts, 1929. Cradock, Cape Province.

Macroscelides proboscideus chiversi Roberts, 1933: 265. 76 miles north of Upington, Cape Province.

Macroscelides proboscideus langi Roberts, 1933: 265. Vlermuisklip, Van Rhynsdorp Dist., Cape Province.

Macroscelides typicus isabellinus Shortridge & Carter, 1938. Port Nolloth, Cape Province.

- Macroscelides typicus ausensis* Roberts, 1938 : 231. 20 miles north of Aus, S.W. Africa.
Macroscelides typicus harei Roberts, 1938 : 232. Brospan, midway between Brandvlei and Van Wyk's Vlei, Cape Province.
Macroscelides typicus brandvleiensis Roberts, 1938 : 232. Brandvlei, Cape Province.
Macroscelides typicus calvinensis Roberts, 1938 : 232. 15 miles east of Calvinia, Cape Province.
Macroscelides proboscideus flavicaudatus Lundholm, 1955 : 285. 6 miles from the mouth of the Omaruru River, South West Africa.

SPECIMENS EXAMINED. Ten skins and seven skulls from South West Africa (Berseba) ; eight skins and four skulls from Cape Province (Deelfontein and Klipfontein) ; the type of *M. melanotis* (skin and skull) ; two in spirit (and one of these skeletonized) from " Bushmanland ".

DESCRIPTION (in amplification of the generic characters given above and the characters listed in Table 1). Length of head and body about 110 mm. (104-115) ; length of tail about 120 mm. (115-130 ; mean 108% of head and body) ; length of hind feet 32-35 mm. ; length of ear 19-22 mm. ; length of snout, from incisors, about 12 mm. Pelage very long, about 17 mm. long dorsally, softer than in any other species, scarcely distinguishable in colour from that of *Elephantulus edwardi* and *E. rupestris* ; light greyish brown dorsally becoming a purer yellowish-brown on the flanks and changing fairly abruptly to white ventrally ; all hairs black for proximal three-quarters or more. Distinguished from *Elephantulus* spp. by absence of any strong tinge of buff behind the ears. Tail bicoloured proximally, black tips of hairs increasing in length distally so that distal half is uniformly black above and below, with the hairs completely obscuring the scales. Ear with the supratragus and tragus large, thin and almost naked (Text-fig. 8a). Claw of hallux reaching half-way to margin of distal pads. Inflation of auditory region of skull extending dorsally to leave a sagittal gap of about 4 mm., and forwards in the pterygoid region as far as the posterior edge of the palate. Rostrum very short, teeth crowded (Text-fig. 9a). I¹ unicuspid ; I² to P¹ about equal in size, clearly bicuspid, incisors with one, canine with two roots ; P² molariform with two prominent lingual cusps ; P⁴ and M¹ equal and largest. Mandible short and deep with the teeth closely crowded. I₂ to P₁ subequal, obscurely two- or three-lobed ; P₂ and P₃ narrow, sectorial ; P₄ largest.

RANGE (Text-fig. 2). The subdesert steppes of Cape Province and South West Africa, extending northwestwards at least to the Omaruru River (22° S.) and southeastwards to Grahamstown, apparently avoiding the coastal macchia zone. Probably not extending north of the upper Orange River. Sympatric throughout its range with *Elephantulus edwardi* and/or *E. rupestris*, but probably not overlapping extensively with *E. myurus* in the northeast, nor with *E. intufi* in the northwest.

The range is divided into two by the Orange River, but in each of the two parts it is likely to be continuous.

Claims that this species extends further north are based on two pieces of evidence : (1) the type specimen of *M. melanotis* which is labelled " Damaraland ", and (2) the record of this species having been collected at Benguela, Angola by Monteiro, quoted by Sclater (1900) and Roberts (1951). This latter claim can be immediately dismissed : the specimen (in spirit in the British Museum) has been labelled *M.*

proboscideus but is in fact an *Elephantulus intufi*. The type of *melanotis* has been examined and is undoubtedly a *Macroscelides proboscideus*. Allowing for the poor condition (the skin, now dry, was probably in alcohol originally and the skull is represented only by the rostrum and mandibles, with very worn teeth), it is not distinguishable from the series from Namaqualand and from Deelfontein. (There is no indication of the "pale reddish brown chest" of the original description, but that part of the skin is very tattered and dirty). There is no reason for assuming that this specimen came from Damaraland. It was described by Ogilby (1838) as having been "procured by Captain Alexander during his recent journey into the country of the Damaras". But Alexander's journey started and finished at Capetown!

SUBSPECIFIC VARIATION. Roberts (1951) recognized nine subspecies in addition to the enigmatic *melanotis*. These were all diagnosed by trivial differences in the shade of the pelage and in average size and there was no implication that any of them represent objective subspecies or anything more than arbitrary samples from a system of continuous variation. Shortridge used the name *melanotis* for all the animals from South West Africa, i.e. from north of the Orange River, and claimed that they differed from true *proboscideus* in having black ears, as opposed to brown, and longer, darker tails. Series examined from Berseba (South West Africa—nine specimens), Klipfontein (Little Namaqualand—five specimens) and Deelfontein (central Cape Province—three specimens), the last two being south of the Orange River, show no differences in size, length and pelage of tail, nor in the colour of the ears (in dry skins). There is a very slight difference in colour, the specimens from Deelfontein being rather more yellow and less grey than the others, but judging from Roberts' description of the other forms this character shows no consistent pattern of variation.

M. p. flavicaudatus is known from two specimens from the Omaruru River, about 500 km. north of the nearest known locality. It is characterized by the very pale dorsal pelage and tail: "The tail of the male is whitish, with the end pale yellowish and covered with long hairs. In the female the tail is yellowish brown and only the very base is whitish." (Lundholm, 1955). It is therefore a distinctive race on the basis of present knowledge and it seems probable that it may represent an isolated northern segment of the species.

Genus *ELEPHANTULUS*

Macroscelides Smith, 1829 (in part).

Elephantulus Thomas & Schwann, 1906: 577. Type-species *Macroscelides rupestris* Smith.

Elephantomys Broom, 1937. Type-species *E. langi* Broom.

DIAGNOSIS. Auditory bullae not grossly inflated; hallux present; three pairs of mammae.

CONTENTS. Nine species.

DELIMITATION OF THE SPECIES. *E. rozeti* of northwestern Africa is an isolated and clearly defined species. The suggestion of Ellerman & Morrison-Scott (1951) that it is conspecific with *E. rufescens* of East Africa was quite unjustified.

Amongst the group with three lower molars, previously placed in a genus or subgenus *Nasilio*, the only discontinuity of variation suggesting specific rank is between *E. fuscipes* of western Uganda and adjacent regions and the remainder, which can be considered a single species, *E. brachyrhynchus*. The latter includes the forms *brachyurus* and *molosae* which were given specific rank by Allen (1939).

Allen (1939) listed eight other species from East Africa. Of these all but one (*E. revoili* of Somalia) appear to represent a single species showing considerable regional variation, mostly clinal, the earliest name being *E. rufescens*.

The remaining forms in southern Africa have caused a great deal of confusion. Smith (1836, 1838) described and illustrated three species of this group, namely *edwardi*, *intufi* and *rupestris*, with type localities, "Oliphant's River", "Flats beyond Kurrichane" (i.e. Marico district, W. Transvaal), and "mountains near the mouth of the Orange River". Specimens bearing these names, but all labelled simply "South Africa", came to the British Museum. The two labelled "*Macroscelides rupestris*" were subsequently marked "cotype" by Thomas. Allen (1939) listed five species, namely *capensis*, *edwardsii*, *intufi*, *rupestris* and *vandami* (*capensis* and *vandami* having been described by Roberts in 1924). Roberts (1951) recognized nine species, namely *barlowi*, *capensis*, *edwardi*, *intufi*, *kobosensis*, *myurus*, *namibensis*, *rupestris* and *vandami*. This differed from Allen's list in the addition of *barlowi*, *kobosensis* and *namibensis*, all described by Roberts in 1938, and by the recognition of *myurus* as a distinct species (listed as a race of *E. rupestris* by Allen). Ellerman *et al.* (1953) reduced the entire group to two species, *intufi* and *rupestris*, which bear almost no relation to the species of previous authors. These were described as a more western species, *intufi*, with P² molariform, and a more eastern species, *rupestris*, with P² sectorial. This drastic change from Robert's classification was due to the realization that the so-called cotypes of *rupestris* in the British Museum had P² sectorial and therefore did not correspond to Robert's conception of *rupestris*. This is indeed the case, but there is no evidence that these specimens came from the type locality of *rupestris* and they do in fact agree perfectly with *E. myurus*, a species not recognized by Smith, and which has not subsequently been found anywhere near the mouth of the Orange River. The name *rupestris* can therefore be retained for the species with molariform P² found in that region. *E. intufi* also has P² molariform but differs from *E. rupestris* in size and pelage. Two other species can be recognized, differing from *rupestris* and *intufi* in having P² sectorial and the ectotympanics greatly swollen. These are a northern one, which is *E. myurus*, and a southern one, which we consider to be *E. edwardi* of Smith and *E. capensis* of Roberts. Roberts (1951) has disputed this synonymy and there are in fact some discrepancies between Robert's *capensis* and Smith's description and figure of *edwardi*. But topotypical specimens of *capensis* do agree closely with the type of *edwardi* and with a considerable number of specimens labelled *edwardi* received by the British Museum from Edward Verreaux after whom the species was named. All these, including the type, are only labelled "South Africa". The lack of close agreement with Smith's figures can probably be explained by the confusion in obtaining specimens for illustration, reported by Smith himself (1838 : text to Plate 15).

KEY TO THE SPECIES OF *ELEPHANTULUS*

- 1 Pectoral gland present (naked or short-haired patch in centre of thorax) 2
 - Pectoral gland absent 4
 2 Prominent brown mark behind eye; two lower molars (i.e. ten lower teeth) 3
 - No brown mark behind eye; three lower molars *E. fuscipes* (p. 102)
 3 Hair of tail becoming long towards the tip, forming a brush; tail about 120 per cent of head and body; I² equal in size to I¹ and I³ *E. revoili* (p. 88)
 - Hair of tail not forming a brush; tail about equal to head and body; I² much smaller than I¹ *E. rufescens* (p. 82)
 4 Tail usually shorter than head and body; three lower molars (i.e. eleven lower teeth) *E. brachyrhynchus* (p. 97)
 - Tail not shorter than head and body; two lower molars 5
 5 P¹ with a lingual cusp; P² molariform, with *two* well developed lingual cusps (Text-figs. 7a and b); ventral pelage superficially white 6
 - P¹ lacking a lingual cusp; P² sectorial with or without *small* lingual cusps (Text-figs. 7c and d); ventral pelage showing grey (except in the North African *E. rozeti*) 7
 6 Size larger (upper tooth row usually over 18.7 mm.); tail about 115% of head and body, distinctly tufted towards the tip, predominantly black above; white eye-ring narrow, broken above and below the eye; P₂ and P₃ with three cusps, arranged in a triangle, behind the principal cusp *E. rupestris* (p. 90)
 - Size smaller (upper tooth-row usually under 18.7); tail about 105% of head and body, not distinctly tufted, speckled above; white eye-ring conspicuous and unbroken; P₂ and P₃ with only two cusps, arranged transversely, behind the principal cusp *E. intufi* (p. 89)
 7 Ectotympanic parts of bullae inflated to same level as entotympanic parts (Text-fig. 6c); I₂ equal to I₁ and I₃ (southern Africa) 8
 - Ectotympanic parts of bullae much less inflated than entotympanic parts (cf. Text-fig. 6b); I₂ larger than I₁ and I₃ (North Africa) *E. rozeti* (p. 76)
 8 P² with one, occasionally two, lingual cusps (Text-fig. 7c); P₁ with two roots; supratragus small and fairly thick; premaxillary suture slightly sinuous (Text-fig. 9h); tail bicoloured throughout its length, yellow-brown above, entirely short-haired *E. myurus* (p. 93)
 - P² without a lingual cusp (Text-fig. 7d); P₁ with a single root; supratragus large and thin (Text-fig. 8c); premaxillary suture straight (Text-fig. 9i); tail black above, distal half black all round and slightly tufted. *E. edwardi* (p. 96)

Elephantulus rozeti

Macroscelides rozeti Duvernoy, 1833. Near Oran, Algeria.

SYNONYMY. Under subspecies.

DESCRIPTION. See Table I for diagnostic characters. This species shows no very close resemblance to any other. It differs from the nearest East African species (*E. rufescens* and *E. revoili*) in lacking a pectoral gland and a distinctive facial pattern, in having the rhinarium naked, P² narrower and in the auditory bullae in which the anterior (alisphenoid) part is almost as large as the posterior (tympanic) part.

The length of head and body is about 110 mm. (90-130); tail about 120 mm. (about 110% of head and body); hind feet about 33 mm. (29-37); ear about 26 mm. (23-30); snout (from incisors) about 15 mm. The pelage is about 14 mm. long dorsally, the proximal three-quarters black, the overall colour varying from

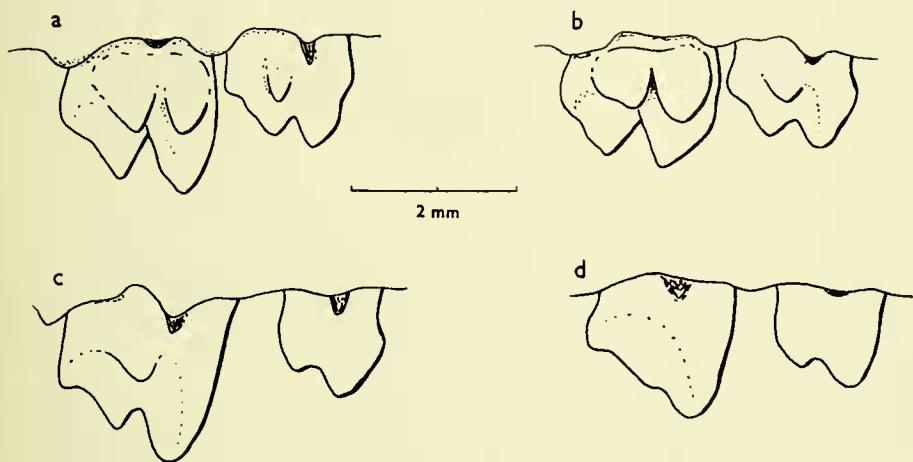


FIG. 7. Lingual aspect of P¹ (right) and P² (left) of *Elephantulus* spp., viewed from a little below the horizontal. (a) *E. rupestris* (B.M. 25.1.2.33); (b) *E. intufi* (B.M. 28.9.11.72); (c) *E. myurus* (B.M. 9.1.20.11); (d) *E. edwardi* (B.M. 1417a).

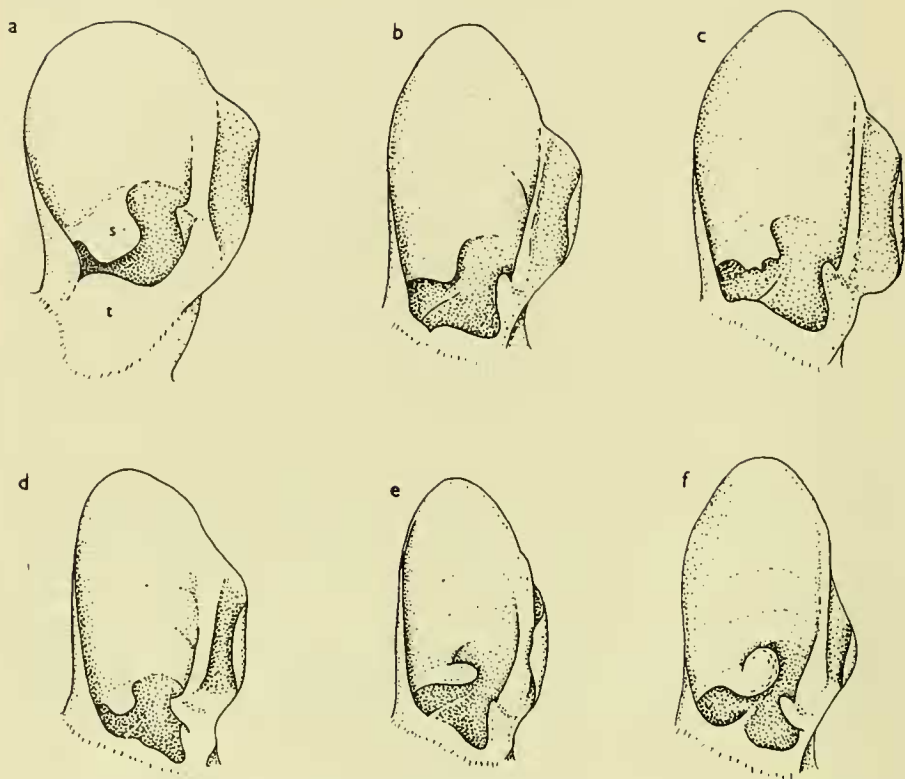


FIG. 8. Left ear of (a) *Macroselides proboscideus* (B.M. 12.4.25.18); (b) *Elephantulus rufescens* (B.M. 36.11.4.67); (c) *E. edwardi* (B.M. 66.3565); (d) *E. brachyrhynchus* (B.M. 63.1009 from Angola—supratragus typical); (e) *E. brachyrhynchus* (B.M. 58.6.18.16 from Mozambique—supratragus atypical); (f) *E. fuscipes* (B.M. 84.5.1.6, the type). Hair is not shown except to indicate the limit of the body pelage. *s*: supratragus; *t*: tragus.

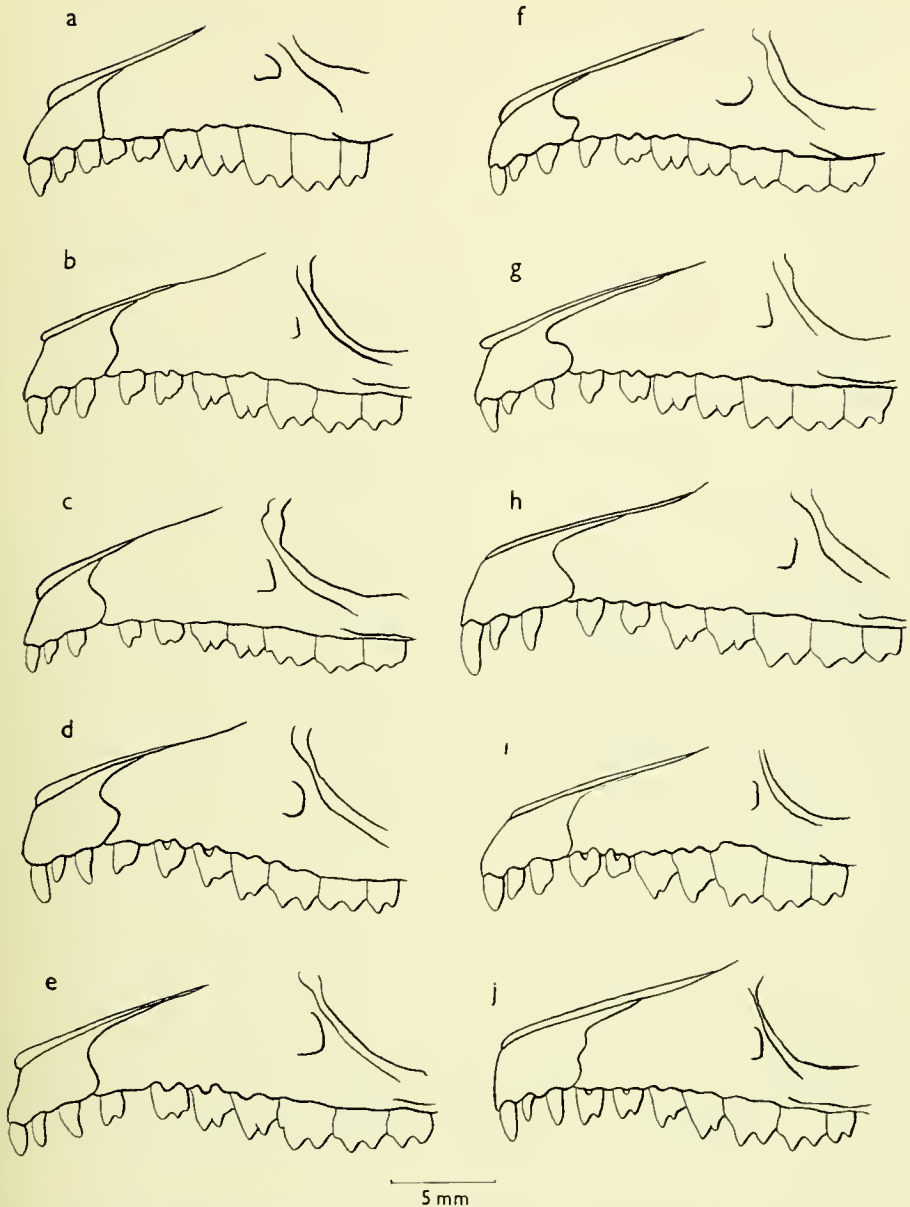


FIG. 9. Left profile of rostrum with permanent dentition. (a) *Macroscelides proboscideus* (B.M. 4.2.3.14); (b) *Elephantulus brachyrhynchus* (B.M. 13.10.18.19); (c) *E. fuscipes* (Tervuren 8957); (d) *E. rufescens* (B.M. 51.406); (e) *E. revoili* (B.M. 5.3.2.3); (f) *E. intufi* (B.M. 28.9.11.72); (g) *E. rupestris* (B.M. 25.1.2.55); (h) *E. myurus* (B.M. 9.1.20.11); (i) *E. edwardi* (B.M. 1.7.9.3); (j) *E. rozeti* (B.M. 27.3.9.1).

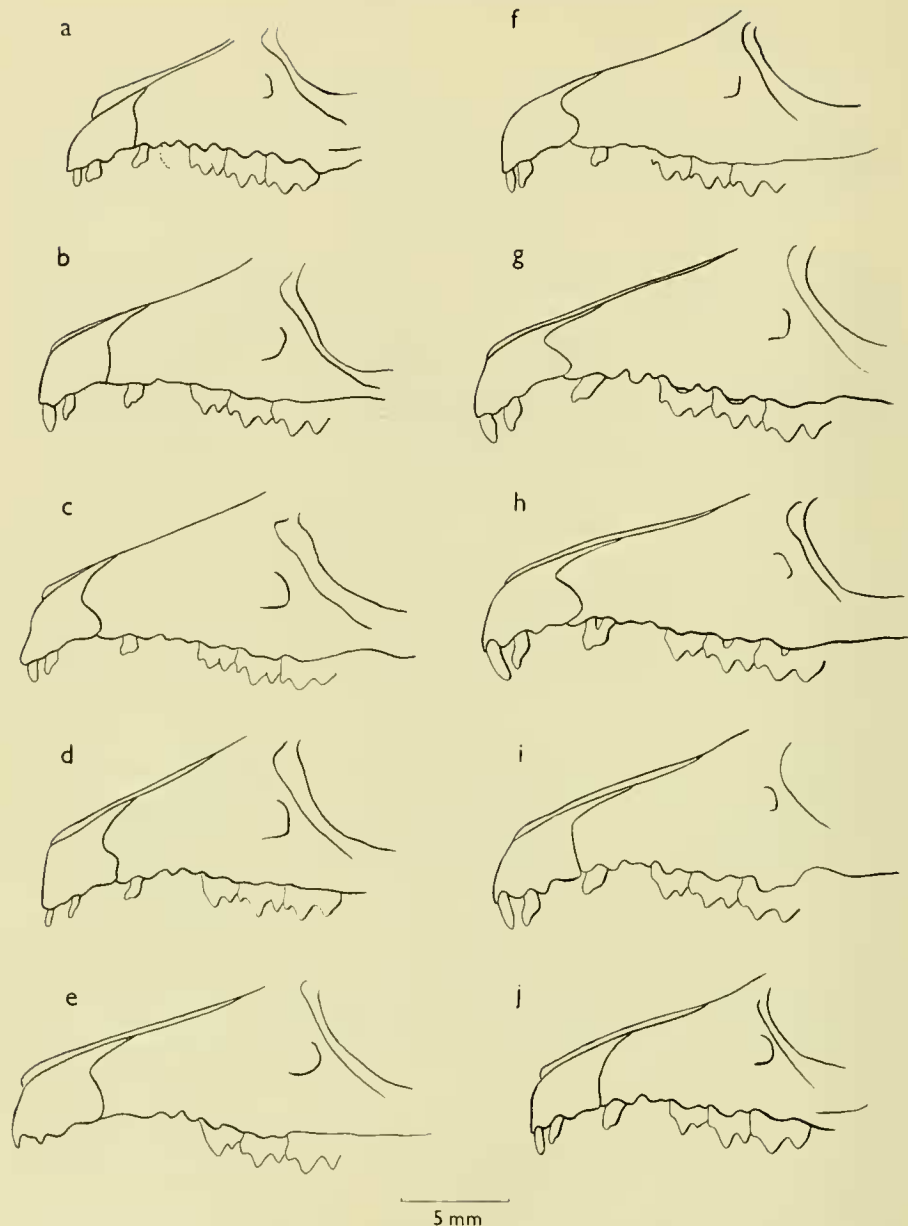


FIG. 10. Left profile of rostrum with deciduous dentition. Deciduous teeth are shown by continuous lines, permanent teeth by dotted lines. (a) *Macroscelides proboscideus* (B.M. 2.9.1.18); (b) *Elephantulus brachyrhynchus* (B.M. 26.5.12.24); (c) *E. fuscipes* (B.M. 84.5.1.6, the holotype); (d) *E. rufescens* (B.M. 64.514); (e) *E. revoili* (B.M. 97.8.9.5); (f) *E. intufi* (B.M. 28.9.11.62); (g) *E. rupestris* (B.M. 1.7.9.2); (h) *E. myurus* (B.M. 1.7.9.5); (i) *E. edwardi* (B.M. 7.1.1.3); (j) *E. rozeti* (B.M. 67.187).

yellowish brown to pale pinkish buff, yellower on the flanks above the fairly sharp transition to the white ventral pelage. The proximal zone of the ventral pelage is black giving a slight greyness to the surface appearance. The subcaudal gland is especially well developed. The diploid chromosome number is 28 (Matthey, 1954).

RANGE (Text-fig. 12). The Mediterranean and subdesert zones of northwestern Africa from southwestern Morocco to Tunisia and Tripolitania. It has been recorded from sea-level up to 1,100 m. *E. rozeti* is unique amongst the Macroscelididae in having no contact with any other species of the family, which may allow a wider range of habitats to be occupied. The Atlas Mountains divide the western part of the range into a coastal region with typical Mediterranean climate, and a drier southern region continuous with the desert. In northeastern Algeria and Tunisia the range is more likely to be continuous from the coast to the edge of the desert.

REGIONAL VARIATION. From western Morocco twelve specimens are available from nine localities, including the types of *atlantis* and *moratus*. These names were based on slight differences of size and colour, but the group as a whole cannot be divided on this basis. Six skins from Oran (topotypical *rozeti*) could not be clearly separated from the Moroccan series although they were inclined to be rather darker. There is therefore no reason to recognize more than one race in the coastal part of the range. From the southern slopes of the Algerian Atlas twenty-two specimens are available from the area north and south of Biskra (including the type of *deserti*) and six from Guel't-es-Stel (including the type of *clivorum*). These cannot be clearly separated into two groups, but together they are distinguishable from the coastal form by their smaller size and pale, sandy colour. The size difference can be most accurately assessed by the length of the upper tooth-row. Taking 17.45 mm. as the dividing line, this separates 86% of the *E. r. rozeti* ($n = 14$) from 87% of the *E. r. deserti* ($n = 23$). It is unlikely that the two groups are completely isolated, but provisionally they can be treated as distinct subspecies dignosed as follows, all measurements referring to individuals with complete permanent dentition.

E. r. rozeti

Elephantulus rozeti moratus Thomas, 1913: 587. Jebel Chedar, about 80 km. southeast of Mazagan, S.W. Morocco.

Elephantulus rozeti atlantis Thomas, 1913: 587. North slope of Great Atlas, south of Seskawa, Ain Moussa, Morocco.

DESCRIPTION. Head and body 113-130, mean 121; tail 127-140, mean 132; hind foot 33-37, mean 34.4; upper tooth-row 17.0-18.8, mean 17.8; dorsal pelage darker, brown tips of hairs about 2 mm. long.

RANGE. Morocco and Algeria north of the Atlas.

E. r. deserti

Macroscelides rozeti deserti Thomas, 1901b. Near Jebel Bourzel, Biskra, Algeria.

Elephantulus deserti clivorum Thomas, 1913: 588. Guel't-es-Stel, E. Algeria.

DESCRIPTION. Head and body 90-120, mean 105; tail 95-128, mean 117; hind foot 29-33, mean 31.7; upper tooth-row 16.5-17.6, mean 16.9; dorsal pelage pale greyish buff, brown tips 3-4 mm. long.

RANGE. Tunisia and Algeria south of the Atlas.

Elephantulus rufescens

Macroselides rufescens Peters, 1878. Ndi, Taita, Kenya.

Macroselides pulcher Thomas, 1894: 69. Usambiro, south of Lake Victoria, Tanzania.

Macroselides boranus Thomas, 1901a. Mega, Ethiopia (4° S.). Not Kenya (Moreau *et al.*, 1946).

Macroselides peasei Thomas, 1901b. Hoolul, 30 miles northwest of Harar, Ethiopia.

Macroselides somalicus Thomas, 1901c. Arabsiyo, 25 miles northwest of Hargeisa, Somalia.

Elephantulus dundasi Dollman, 1910. Harich, near Lake Baringo, Kenya.

Elephantulus phaeus Heller, 1910. Sotik dist., Kenya (0° 52' S., 35° 25' E.).

Elephantulus delicatus Dollman, 1911. Mt Nyiro, Orr Valley, Kenya.

Elephantulus pulcher vendilis Lönnberg, 1912. Near Chanler Falls, Kenya.

Elephantulus rufescens mariakanae Heller, 1912. Mariakani, Kenya (3° 52' S., 39° 29' E.).

Elephantulus ocularis Kershaw, 1921. Dodoma, Tanzania.

Elephantulus renatus Kershaw, 1923a. Gwao's, near Itiga, Singida, Tanzania.

Elephantulus rufescens hoogstraali Setzer, 1956. Ikote, Sudan (4° 05' N., 33° 04' E.).

TAXONOMIC STATUS. A clearly defined species, not closely resembling any other except *E. revoili*.

SPECIMENS EXAMINED. Ethiopia ten (including five received on loan from Oklahoma State University); Kenya 102 (including nine in the National Museum, Kenya); Somalia eighteen (including seven received on loan from the University of Florence); Sudan five; Tanzania thirty-four (including two received on loan from Berlin Museum, and six in the museum of the College of Wildlife Management, Mweka, Tanzania); Uganda ten.

DESCRIPTION. See Table 1 for diagnostic characters and Text-figs. 8b, 9d and rod for structural details. *E. rufescens* is closely similar to *E. revoili* with which species alone it shares the presence of a hairy rhinarium and distinctive facial pattern. The last feature gives these species a very close resemblance to the much larger *Petrodromus tetradactylus* which meets *E. rufescens* in parts of Tanzania and Kenya, and it is also of interest to note that in *Petrodromus* there is often a naked or shortly haired area apparently representing a vestigial pectoral gland. *E. rufescens* differs from *E. revoili* in its smaller size (see Text-fig. 13), shorter and less hairy tail, small I², and in the dorsal pelage which everywhere shows considerably more yellow than does that of *E. revoili*. The subcaudal gland is rather rudimentary being represented by a slight ridge in the mid-ventral line of the proximal part of the tail. The pectoral gland is fringed by short, wholly white hairs, quite different from the surrounding pelage.

RANGE (Text-fig. 11). The dry woodland and steppe zones of East Africa from Tanzania (south at least to the River Ruaha) northeastwards through Kenya to Somalia and eastern Ethiopia; and northwestwards as far as eastern Uganda and the extreme southern region of Sudan. In Tanzania there is one record from the

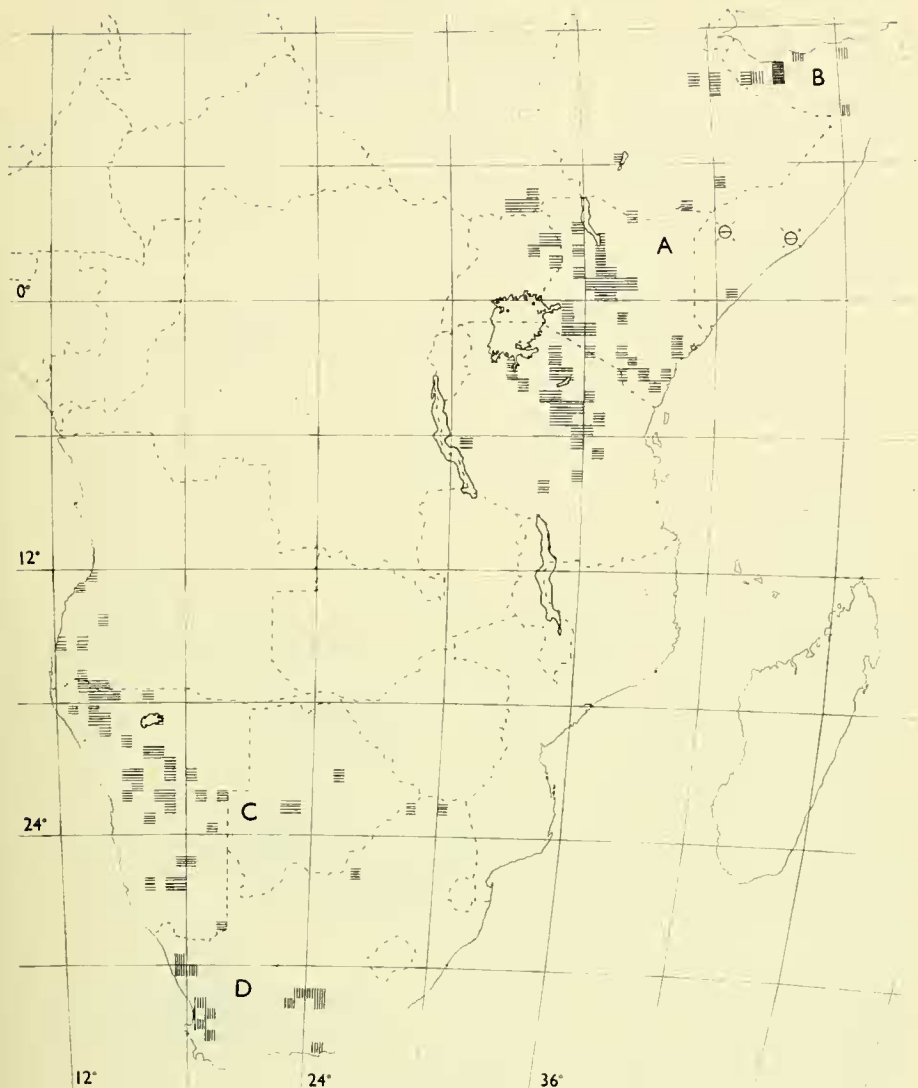


FIG. 11. Recorded distribution of A: *Elephantulus rufescens*; B: *E. revoili*; C: *E. intufi*; D: *E. edwardi*. The circles indicate approximate localities of *E. rufescens*.

extreme west from Katavi Mbuga (c. $6^{\circ} 45' S.$, $30^{\circ} 50' E.$), given, without details, by Swynnerton and Hayman (1951). Comparison with a vegetation map suggests that this may be an isolated population. In Tanzania the range of *E. rufescens* abuts that of *Petrodromus tetradactylus* but there may well be a clear difference in



FIG. 12. Recorded distribution of A: *Elephantulus rozeti*; B: *E. rupestris*; C: *E. myurus*.

habitat, the *Elephantulus* being in the more open grassland and the *Petrodromus* in woodland. In Kenya the range overlaps that of *E. brachyrhynchus*, but here also there is probably a difference in habitat, *E. brachyrhynchus* being confined to the wetter woodland. In Uganda there is no evidence of precise overlap with *E. brachyrhynchus* and *E. fuscipes*, which replace *E. rufescens* entirely in the wetter

western parts of the country. In Somalia *E. rufescens* is probably replaced by *E. revoili* in the drier parts of the north and east.

Judging by the distribution of the wooded steppe zone occupied by *E. rufescens*

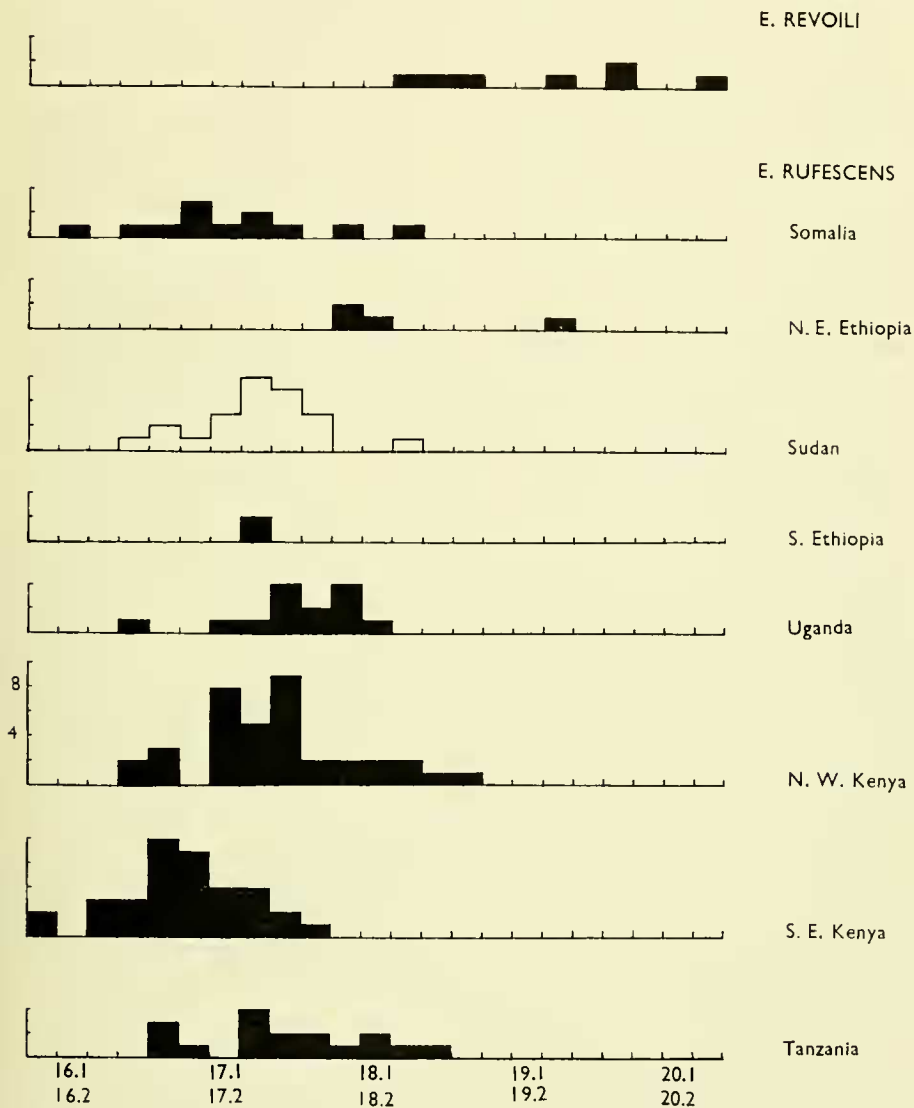


FIG. 13. Variation in length of the upper tooth-row of *Elephantulus revoili* and *E. rufescens*. The data for the Sudan were supplied by Dr. H. Setzer from specimens in the U.S. National Museum.

there is no reason to suspect the presence of any gross discontinuities in the range except in the southwest and perhaps in the mountains of Ethiopia. However, it is narrowly constricted by the subdesert of northern Kenya which, along with the Tana River, may effectively isolate the northern and southern populations.

REGIONAL VARIATION (Text-fig. 13). In view of the probable continuity of distribution it is unlikely that any objective subspecific boundaries can usefully be recognized. No significant variation can be detected in cranial characters nor in external measurements except that the available specimens from Ethiopia are rather large. All previous subspecific descriptions have been based almost entirely on colour. This undoubtedly varies considerably throughout the range, but the existing collections are sufficient to suggest that most of this variation is clinal.

In Tanzania no specimen has been examined from the presumably isolated southwestern population, but samples are available from four other widely spaced regions. Comparing the samples from the southernmost locality, Dodoma (thirteen skins including the type of *ocularis*) and from Mwanza, south of Lake Victoria (six skins, including the type of *pulcher*) the difference in colour is fairly clear-cut, *ocularis* being rather yellowish above and on the flanks whilst *pulcher* is much greyer. Ventrally *ocularis* has the dark basal zone of the hairs very short or completely absent whilst in *pulcher* it is prominent. However, four skins from intermediate localities, including the type of *renatus*, are rather variable and, on the whole, intermediate between *ocularis* and *pulcher*. A single specimen from Kibaya (5° 17' S., 36° 34' E.), northeast of Dodoma, is a deeper yellowish brown, linking *ocularis* with *rufescens* s.s. of southeastern Kenya. All the skins from Tanzania are characterized by a more prominent white eye-ring than is found in Kenya, especially the white streak between the eye and the ear.

Within Kenya the twelve skins from the vicinity of Voi, i.e. nearly topotypical *rufescens*, are noticeably more rufous than any others (except the Ethiopian *boranus*—see below). This can probably be considered as an adaptation to the colour of the local soil, which is very dark red. All the other available specimens from Kenya are less rufous and show very little variation amongst themselves. These include series from Taveta (eight skins) and from near Archer's Post on the northern Uaso Nyiro (nineteen skins). All these have hitherto been referred to *dundasi*. Specimens from further north (in the Northern Frontier District) are noticeably paler, being very similar in colour to *ocularis* of Tanzania, which they also resemble in the prominence of the eye-ring and in the tendency to lack the dark bases in the ventral pelage. The type of *delicatus* represents this form and is further characterized by the very long tail.

North of the subdesert zone of northern Kenya, from which *E. rufescens* is probably absent, specimens are available from three main regions; the extreme southern (coastal) area of Somalia; several montane areas in southern Ethiopia; and northeastern Ethiopia and the adjacent parts of Somalia. In eastern Kenya a single specimen from the Tana River is considerably greyer than all the other Kenya specimens and this greyness is even more marked in a series from southern

Somalia (0° 26' N., 42° 48' E.). The five specimens available from southern Ethiopia fall into three groups. The type of *boranus* from Mega on the southern border (1,370 m.) is a very rufous form almost indistinguishable from topotypical *rufescens*, but even deeper in colour. The other three from further east (Farda Robo and Murri) are less bright and are virtually indistinguishable from the *dundasi* of Kenya, being darker than those from the N.F.D. A single skin from Lake Abaya (1,300 m.) is much greyer than these, with a more clearly defined dorsal stripe and almost black post-ocular spots and upper surface of the tail. These characters are unique in the species.

Specimens from northern Somalia (*somaticus*) are again very yellow dorsally, a little more so than those from northwestern Kenya. The form *peasei* from north-eastern Ethiopia, only about 200 km. from the *somaticus* group, is represented by the type and by five other skins and skulls borrowed from the Oklahoma State University. It is distinctly different from *somaticus*, being very grey above and showing very little yellow even on the flanks. (In fact the types of *peasei* and of *renatus* from Tanzania are scarcely distinguishable). They are also rather large and one of the four measurable skulls is exceptionally large (condylobasal length 37.3, upper tooth-row 19.3 mm.). The buff patches behind the ears, present in all *E. rufescens*, are especially noticeable in contrast to the grey back. Since there is no obvious barrier separating these two forms they are likely to be connected by intermediates. The types of *peasei* and *somaticus* were both collected at 2,400 m.

The only described forms of *E. rufescens* that have not been examined are *phaeus*, *rendilis*, *marikananae* and *hoogstraali*. *Phaeus*, from southwestern Kenya, was described as being "closely allied to *pulcher* from which it differs in the darker umber-brown colour, being 'grey-fawn' only on the sides". This is consistent with the view that it is intermediate in colour, as well as geographically, between *pulcher* and *dundasi* of central Kenya. *Rendilis*, from the Uaso Nyiro, was described entirely on the basis of colour, the ventral hair being white to the roots and the post-ocular streak pale by comparison with *pulcher*. This form is therefore represented by a nearly topotypical series available from Archer's Post, which are scarcely separable from *dundasi*. *Mariakananae*, from near Mombasa, was compared with *pulcher* and *rufescens* and described as intermediate between these forms in colour, no other characters being described. *Hoogstraali* was described, compared with *dundasi* of northwest Kenya, as having the belly white, tail and hind feet long, dorsal colour dark and post-ocular spot more prominent. One specimen available from the Didinga Mountains, about 70 km. east of the type locality of *hoogstraali*, fits this description but at the same time is only marginally separable from the type of *dundasi* and from a series from Karamoja, Uganda. *Hoogstraali* represents the northwestern extremity of the range, but there is no reason to suppose that it is geographically isolated.

None of these descriptions is inconsistent with the overall pattern of regional variation outlined above. Few are likely to represent isolated populations and no abrupt discontinuities of variation have been demonstrated. The difference between *peasei* and *somaticus* is the nearest approach to such a discontinuity.

Elephantulus revoili

Macroselides revoili Huet, 1881. Medjourtine, i.e. northeastern Somalia. Holotype: Paris Museum, 1881-II, mounted skin.

TAXONOMIC STATUS. A clearly defined species, closely related only to *E. rufescens*.

SPECIMENS EXAMINED. Fifteen, including two received on loan from the University of Florence.

DESCRIPTION. See Table 1 for diagnostic characters. Head and body 122-148, mean of six 132; tail 144-167, mean of six 157 (119% of head and body); hind foot 34-39, mean of six 37.3; ear 24-26; upper tooth-row 18.4-20.4, mean of eight 19.1 (Text-fig. 13).

E. revoili differs from *E. rufescens* only in its long hairy tail, large size, pale pelage and large 1². Two small juveniles have the dorsal pelage paler than that of the adults, with more yellow and less grey. The pectoral gland is present in every individual and is marked by dense fringes of short white hair, but in all but one skin no secretion is visible on the surrounding hair, whereas in *E. rufescens* most specimens show extensive staining in the vicinity of the gland. This may have led Heller (1912) to state that the pectoral gland is absent in *E. revoili*.

The caudal hairs are white with brown tips which become longer towards the tip of the tail, forming a dark brush; the dorsal pelage is pale brownish or pinkish grey, when compared with *E. rufescens* rather paler than the form *peasei* but less yellow than *somalicus*, most similar to *E. rozeti deserti*.

RANGE (Text-fig. 11). Specimens in the British Museum are from seven localities, all on or near the north coast of Somalia between 44° and 48° 20' E. The only reliable record away from this area is from Run, Garoe (8° 17' N., 48° 20' E.) (two specimens in the Zoological Museum of the University of Florence). Peel (1900) recorded seeing a specimen at Sinnadogho, Marehan country. This is much further south (5° 15' N., 46° 15' E.), but since *E. rufescens somalicus* had not yet been described and *E. revoili* was thought to be the only species in Somalia, this cannot be treated as a positive record of *E. revoili*.

E. revoili appears to be sympatric with *E. rufescens* at Wagar (10° 01' N., 45° 26' E.) and at Upper Sheikh (9° 56' N., 45° 12' E.), but field notes suggest that the two differ in habitat, *E. revoili* occurring on stony ground and *E. rufescens* being found amongst bushes on sandy soil. The information available is insufficient to determine whether *E. revoili* is confined to the rocky, montane habitats of northern Somalia or whether it is more widespread, replacing *E. rufescens* throughout the drier parts of the country.

REGIONAL VARIATION. No subspecies have been described. The two available skins from Gabadir (10° 24' N., 45° 02' E., 240 m.), one of adult size, the other juvenile, have the dorsal pelage very pale and yellowish. The remaining eight adult skins from the northern part of the range are uniform in colour, and of these five are from localities of known altitude, all over 1,300 m. The two southernmost specimens (Garoe) are a very pale, pinkish buff, the proximal zone of the dorsal hairs being short (rather less than half the length of the hair) and grey, not black as in the northern specimens. Also the black-tipped guard hairs are much fewer.

Elephantulus intufi

Macroscelides intufi Smith, 1836: 42. Flats beyond Kurrichaine, Marico district, western Transvaal. Holotype: B.M. (N.H.) 59.5.7.13 (= 41.799 = 1314a), skin and skull.

Macroscelides alexandri Ogilby, 1838: 5. Damaraland, South West Africa.

Macroscelides brachyrhynchus schinzi Noack, 1889. Ondongastamm, Ovamboland, South West Africa.

Elephantulus intufi kalaharicus Roberts, 1932: 17. Damara Pan, central Kalahari, Botswana.

Elephantulus intufi mossamedensis Hill & Carter, 1937. 101 km. east of Mossamedes, Angola.

Elephantulus namibensis Roberts, 1938: 233. 45 miles north of Aus, South West Africa.

Elephantulus intufi campbelli Roberts, 1938: 234. Barby Farm, 25 miles west of Helmeringshausen, South West Africa.

Elephantulus intufi mchughi Roberts, 1946: 309. Okombahe, Omaruru, South West Africa.

Elephantulus intufi omahehensis Lehmann, 1955. Klein Okaputa, south of Okavango, South West Africa.

Elephantulus intufi canescens Lundholm, 1955: 283. Ohopoho, Kaokoveld, South West Africa.

SPECIMENS EXAMINED. Angola eleven; Botswana one (received on loan from the National Museums of Rhodesia); South West Africa fifty-six (including the type of *alexandri*); Transvaal one (type of *intufi*).

TAXONOMIC STATUS. As understood here, this species agrees with *E. intufi* of Roberts (1951) with the addition of his *E. namibensis*. Ellerman *et al.* (1953) included in *E. intufi* all the forms included by us, but also all those that we include in *E. rupestris*.

DESCRIPTION. See Table 1 for the diagnostic characters and Text-figs. 7b, 9f and 10f for cranial details. *E. intufi* resembles *E. rupestris*, and differs from the other two southern species, in having P² molariform, with two well-developed lingual cusps; P¹ with a lingual cusp; the ectotympanic less swollen than the entotympanic parts of the bullae; and the ventral pelage white, showing little grey at the surface. It differs from *E. rupestris* in its smaller size (upper tooth-row under 18.7 mm.); relatively shorter, untailed tail (c. 105% of head and body); generally paler and more yellow dorsal pelage; conspicuous and unbroken white eye-ring; and by the absence of an additional cusp on P₂ and P₃ between the principal cusp and the two posterior cusps (indeterminable if the teeth are heavily worn). The bullae are also rather larger and less angular than those of *E. rupestris*; this varies somewhat from region to region but is a useful confirmatory character if both species are available from the same region.

The dorsal pelage is usually yellowish buff with the very long, black-tipped guard hairs contrasting strongly, especially on the rump. The brighter buff patches behind the ears are especially conspicuous. The hairs of the tail are white, only those on the dorsal surface having black tips, giving a speckled appearance. Although they increase in length towards the tip there are very few wholly black as in *E. rupestris*. The ventral pelage shows even less grey at the surface than that of *E. rupestris*.

RANGE (Text-fig. II). Dry savanna woodland, steppe and subdesert of southwestern Angola, the whole of South West Africa except the coastal desert, probably most of Botswana, and the extreme northeastern region of Transvaal. The northern-

most locality is Catumbella, Angola ($12^{\circ} 25' S.$) (specimen in British Museum), the easternmost the Zoutpansberg, North Transvaal (Roberts, 1917), and the southernmost Ariamsvlei near the Orange River (Roberts, 1951).

Through most of South West Africa *E. intufi* is sympatric with *E. rupestris*. The range overlaps slightly with that of *Macroselides proboscideus* in southern South West Africa and touches that of *E. myurus* in the east. Roberts (1917) records a specimen of *E. intufi* from the Zoutpansberg, collected "not far from a place" where the type of *E. myurus mapogonensis* was collected. It also touches upon the range of *E. brachyrhynchus* in the north and probably in the east, both species having been recorded from Quillingues, Angola ($14^{\circ} 05' S.$, $14^{\circ} 04' E.$) and from adjacent areas in western Transvaal.

REGIONAL VARIATION (Text-fig. 14). No specimens from southern South West Africa have been examined and only the type and one other from the eastern part of the range. All the races that have been described have been based on slight variation in colour. It is unlikely that there is any gross discontinuity of range or variation in the central part of the range.

Four skins from Catumbella, Angola are almost identical to the large series examined from the Kaokoveld in northern South West Africa. Lundholm's name *canescens* is available for this group. The type locality of *mossamedensis*, described as being paler than adjacent forms, lies between these areas. Four skins from Ovamboland (east of Kaokoveld) are less grey and more yellow than the Kaokoveld series. Noack's name *schinzi* is available for this form if required. It is clear from his description (Noack, 1889) that this is a form of *E. intufi* rather than of *E. brachyrhynchus* in which it was originally placed (see p. 98). Three from Karabib (*c.* $22^{\circ} S.$) are paler and yellower than the Kaokoveld specimens. These agree well with the type of *alexandri* (from "Damaraland", but in fact it could have come from anywhere in South West Africa) and this form is probably also represented by Roberts' *mchughi*. (A fourth specimen from Karabib, reported by Thomas & Hinton (1925) as *E. intufi*, is in fact *E. rupestris*. These authors described it as being greyer than the others but said nevertheless "there is no doubt that they are really referable to this species" (*E. intufi*). This specimen was again commented upon by Thomas (1926) when he noted that the bullae differed from those of the rest of the series.) If, as seems probable, all these represent one race distinct from the nominate form (which may represent an isolated eastern population), the earliest name is *alexandri*.

Specimens from southern South West Africa (forms *namibensis* and *campbelli* of Roberts) are, according to Roberts, also pale, as is his *kalaharicus* from central Botswana. A single specimen examined from eastern Botswana (near Lethaking) is slightly more pink and less yellow than most western specimens.

Elephantulus rupestris

Macroselides rupestris Smith, 1831. Mountains near the mouth of the Orange River.

Neotype: B.M. (N.H.) 4.2.3.7. skin and skull (see below under "Nomenclature").

Elephantulus vandami Roberts, 1924: 62. Cradock, Cape Province.

Elephantulus barlowi Roberts, 1938: 233. Aus, South West Africa.

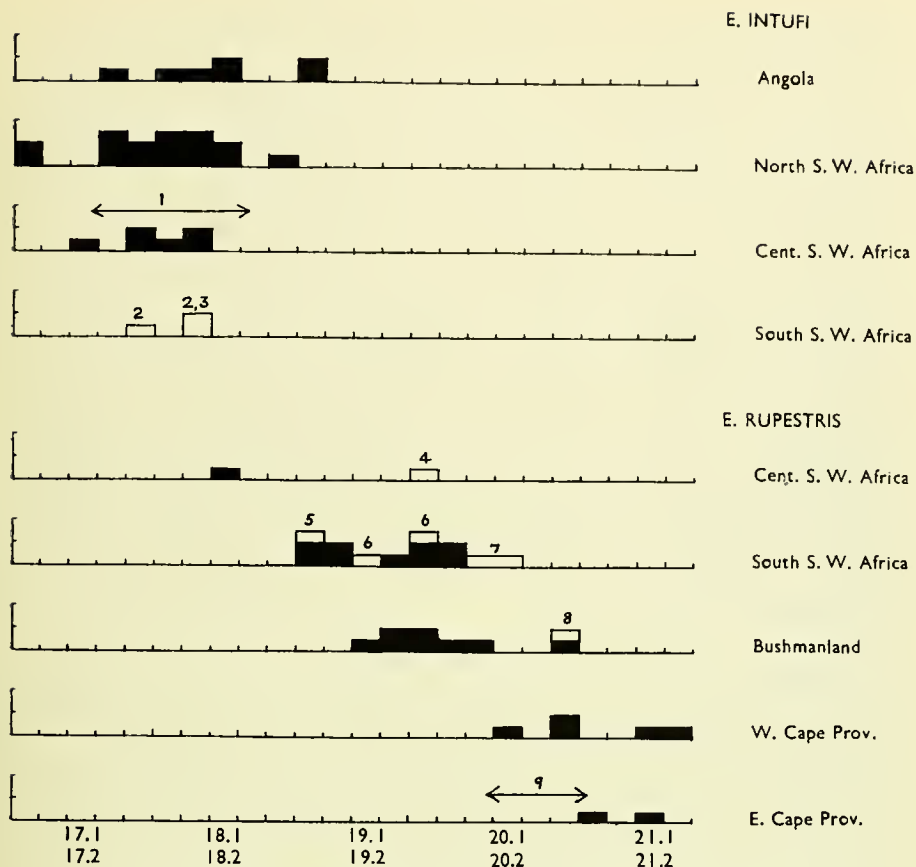


FIG. 14. Variation in length of the upper tooth-row of *Elephantulus intufi* and *E. rupestris*. The open blocks and lines represent data taken from Roberts (1951) as follows: 1: range of 22 *mchughi*; 2: *campbelli* (incl. type); 3: type of *namibensis*; 4: type of *okombahensis*; 5: type of *kobosensis*; 6: *tarri*; 7: type and topotype of *barlowi*; 8: *vandami*; 9: *vandami* (incl. type).

- Elephantulus kobosensis* Roberts, 1938: 233. Kobos, 30 miles southwest of Rehoboth, South West Africa.
- Elephantulus rupestris tarri*, Roberts, 1938: 234. Barby Farm, 25 miles west of Helmeringshausen, South West Africa.
- Elephantulus barlowi okombahensis* Roberts, 1946: 309. Okombahe, Omaruru, South West Africa.
- Elephantulus barlowi gordoniensis* Roberts, 1946: 309, Upington, Cape Province.
- Elephantulus intufi* [part]: Ellerman *et al.* (1953).
- Elephantulus vandami montanus* Lundholm, 1955: 282. Oropembe, Kaokoveld, South West Africa.

SPECIMENS EXAMINED. Cape Province twenty-four (including four from the U.S. National Museum) ; South West Africa sixteen.

NOMENCLATURE. Ellerman *et al.* (1953) included this species in *E. intufi* and used the name *rupestris* for the species that we call *E. myurus* and *E. edwardi*. This error was caused by their acceptance as the type of *rupestris* of one of Smith's specimens in the British Museum labelled "*Macroseelides rupestris*—South Africa" (no. 59.5.7.12). This specimen agrees in every way with *E. myurus*. Since *E. myurus* has not been found anywhere near the mouth of the Orange River (in spite of extensive collecting) and since there is nothing to indicate that the specimen in question came from there, it has no claim to be the type of *rupestris*. In fact none of Smith's specimens in the British Museum is *E. rupestris*, i.e. the species subsequently collected, to the exclusion of all others except *E. edwardi* (of which good type material exists), near the mouth of the Orange River.

In fact none of Smith's specimens of this species, agreeing with subsequent topotypical material, have ever been reported. Most of his original material was lost (Smith, 1838: text to plate 15), and it is probable that topotypical *rupestris* did not survive. In view of the confusion that has been caused by the absence of a genuine type specimen, it would seem wise to designate a neotype. For this we choose number 4.2.3.7 in the British Museum, a skin and skull of an adult male collected at Klipfontein, Namaqualand, Cape Province (29° 13' S., 17° 39' E., 3,100 ft.) on 29th April, 1903 by C. H. B. Grant. This locality is consistent with the original type region.

DESCRIPTION. See Table 1 for diagnostic characters and Text-figs. 6b, 7a, 9g and 10g for cranial details. Head and body about 130 mm.; tail about 140–150 mm., about 115% of head and body; hind feet about 35 mm.; ear about 25 mm. Dorsal pelage greyish brown becoming almost pure grey on the flanks. Buff patches behind ears prominent. Ventral pelage showing more grey on the surface than in *E. intufi* but considerably less than in *E. myurus* and *E. edwardi*. Dorsal surface of the tail including many wholly black hairs which reach 6 mm. long at the tip.

E. rupestris can be distinguished from *E. intufi* by the longer, darker and more tufted tail; slightly greyer ventral pelage; darker, greyer dorsal pelage; less distinct eye-ring; smaller, more angular bullae; and by the presence of an additional cusp on P₂ and P₃, behind the principal cusp (only visible in unworn teeth).

RANGE. See Text-fig. 12. The subdesert steppe of South West Africa, north at least to 18° S.; and of Cape Province, in Little Namaqualand and from Upington to Grahamstown. The northernmost localities are Oropembe and Sanitatas from where Lundholm (1955) described *montanus*. The fact that only four specimens have been obtained in the Kaokoveld, compared with large numbers of *E. intufi*, suggests that it is local, and the same applies to the central area of South West Africa. In the south of South West Africa the opposite is true, *E. intufi* having been collected rarely amongst large numbers of *E. rupestris*. It seems probable that the population in the mountains of Little Namaqualand is isolated from the rest of the species, whilst the southeastern localities are also likely to represent isolated populations.

E. rupestris overlaps with *E. intufi* extensively in South West Africa. It overlaps with *Macroscolides proboscideus* in southern South West Africa (Shortridge (1934) records that the two species live in close contact on the same ground), and in most of its range in Cape Province. It is probably only marginally sympatric with *E. edwardi* and *E. myurus*, the range of *E. rupestris* forming a narrow strip in Cape Province between these other two species. It has been recorded with *E. edwardi* at Witwater, Little Namaqualand (Shortridge, 1942) and with both *E. edwardi* and *E. myurus* at Deelfontein, 31° 00' S., 23° 48' E. (specimens in British Museum). In the latter collection (which also includes *Macroscolides proboscideus*) the single specimen of *E. rupestris* is labelled "Karoo, Deelfontein".

REGIONAL VARIATION. See Text-fig. 14. Insufficient material has been examined from the extremities of the range to assess the validity of the marginal races. All the named forms are based on slight variation in pelage and in size and it seems unlikely that any genuinely discontinuous races exist. Series examined from Little Namaqualand, the Upington district, and Berseba in South West Africa (nearly topotypical *rupestris*, *gordoniensis* and *tarri* respectively) show no variation justifying the recognition of subspecies. Animals from western and northern South West Africa are reported to be pale. This includes the forms *barlowi*, *kobosensis*, *okombahensis* and *montanus*. Only one such specimen is available in the British Museum, from Karabib (about 22° S., 16° E.). Its tail is as tufted as in other *E. rupestris*, but very few of the hairs are wholly black. The dorsal pelage is very pale, but lacks the yellow colour of *E. intufi*.

The southeastern form, *vandami*, is described by Roberts, comparing it with typical *rupestris*, as being browner above, darker grey on the flanks, and having the tail wholly dark at the tip. The five specimens examined, from Deelfontein, and near Beaufort West, do not confirm this and cannot justify subspecific rank. Mr. C. G. Coetzee of the Transvaal Museum has kindly reported on the type of *vandami* and confirmed that it does indeed have the auditory region and P² of *rupestris* as here defined.

Elephantulus myurus

Elephantulus rupestris myurus Thomas & Schwann, 1906. Woodbush, Northeastern Transvaal.

Holotype: B.M. (N.H.) 6.4.3.2, skin and fragment of skull, ♀.

Macroscolides rupestris Smith, 1831 (in part).

Elephantulus rupestris jamesoni Chubb, 1909. Johannesburg, Transvaal.

Elephantulus rupestris mapogonensis Roberts, 1917. Njelele River, north of Zoutpansberg, Transvaal.

Elephantulus rupestris centralis Roberts, 1946: 310. Fauresmith, Orange Free State.

Elephantulus rupestris: Ellerman *et al.*, 1953.

Elephantulus rupestris fitzsimonsi Lundholm, 1955: 184. Nyamaziva Falls, Inyanga area, Rhodesia.

SPECIMENS EXAMINED. Botswana four; Cape Province nine; Orange Free State six; Natal one; Transvaal thirty-five (including the types of *myurus* and *jamesoni*); Rhodesia six (including five in the National Museums, Rhodesia). Eight of the South African specimens were from the U.S. National Museum.

TAXONOMIC STATUS. This species was only recognized as specifically distinct from *E. rupestris* in 1935 (Roberts, 1935), and the species as defined by Roberts (1951) is recognized here. However, Ellerman *et al.* (1953) treated it as conspecific with *E. edwardi* and used for this enlarged species the name *rupestris* because of the reputed type specimen in the British Museum (see p. 92 above). The differences between this species and *E. edwardi* are small but clear-cut and the two species are sympatric in at least one locality (Deelfontein).

DESCRIPTION. See Table 1 for diagnostic characters and Text-figs. 6c, 7c, 9h and 10h for cranial details. Head and body about 120 mm.; tail about 140 mm.; hind foot about 35 mm.; ear about 24 mm. Dorsal pelage dull greyish brown, rather more yellow on the flanks. Ventral pelage with the white tips short, making the overall colour pale grey, much greyer than in *E. rupestris*. Pelage behind ears only faintly differentiated from rest of dorsal pelage by scarcity of black-tipped hairs (but more strongly differentiated in the north of the range). Tail shortly haired throughout, variable in colour.

Externally *E. myurus* can be distinguished from *E. rupestris* by the very much less hairy tail, by the less conspicuous buff patches behind the ears (at least in the south) and by the darker ventral pelage. From *E. edwardi* it can be distinguished by the slightly less hairy tail which is never wholly black above and at the tip (this may *not* apply in some northern parts of the range where *E. edwardi* is absent), and by the slightly lesser contrast between brown back and grey flanks.

The skull of *E. myurus* is easily separated from that of *E. rupestris* and *E. intufi* by the greatly swollen ectotympanics which are level with the entotympanics or nearly so (Text-fig. 6c), by the absence of a lingual cusp on P¹, and by P² which is narrower, usually with only a single small lingual cusp (Text-fig. 7c). Occasionally two small lingual cusps are present but these are always less than half the height of the labial cusps and are usually very close together. The discrepancy in size between the labial cusps of P² is also greater than in *E. rupestris* (cf. Text-figs. 7a and c). From *E. edwardi* it is distinguished by the sinuous suture between premaxilla and maxilla, by the double-rooted P₁, by the larger size (Text-fig. 15), and, less certainly perhaps, by the presence of a lingual cusp on P².

RANGE. See Text-fig. 12. The high grasslands from Deelfontein and Burghersdorp (Cape Province) through Orange Free State and western Natal to northern Transvaal, Rhodesia and eastern Botswana. In northern Transvaal and Rhodesia the range is probably fragmented, being confined to areas of drier grassland or more open montane habitats. Everywhere this species is found especially where outcrops of rock provide cover.

In the southwest the range touches that of *E. rupestris*, *E. edwardi* and *Macroselides proboscideus*, all four species being either sympatric or closely adjacent in the Deelfontein area. In northwestern Transvaal *E. myurus* meets *E. intufi* whilst in northern Transvaal and Rhodesia there is a wider overlap with *E. brachyrhynchus* although there is probably a habitat difference, *E. brachyrhynchus* being on the more wooded ground.

REGIONAL VARIATION. There appears to be no significant variation in pelage

throughout the range. The form *jamesoni* (Johannesburg) was described in comparison with *E. rupestris* rather than *myurus*. Roberts (1951) rejected any difference in pelage between *jamesoni* and *myurus* (with which we agree) but retained *jamesoni* as a race on the basis of its large size. He likewise diagnosed *mapogonensis* (North Transvaal) solely on the basis of its small size. He described *centralis* (from the south of the range) by comparison only with *E. edwardi*. In fact it cannot be distinguished from more northern samples. The only accurate available comparison of size, using upper tooth-row (Text-fig. 15), suggests that size decreases towards the north but provides no grounds for the recognition of discrete subspecies.

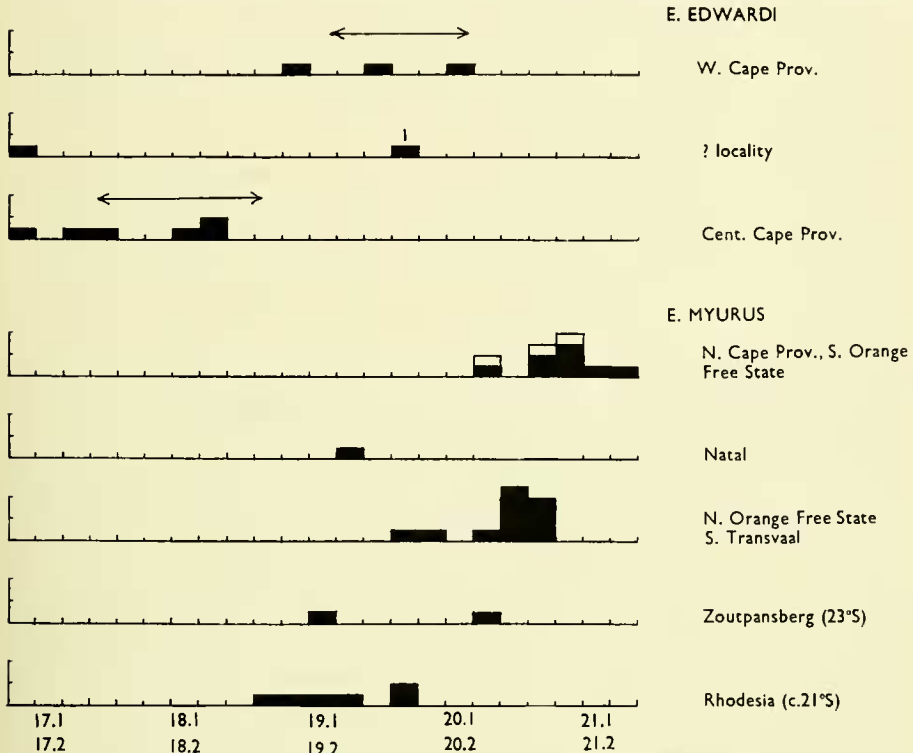


FIG. 15. Variation in length of the upper tooth-row of *Elephantulus edwardi* and *E. myurus*. The lines represent the ranges given by Roberts (1951). 1: type of *edwardi*.

The form *fitzsimonsi* (Inyanga area, Rhodesia) is based on a single specimen with greyish back, pale post-auricular patch and black dorsal surface of the tail. It is probably an isolated form and may be a valid race. The only specimens examined from Rhodesia, one from Matopos and five from the Lundi River, do not show these characters and are scarcely distinguishable from Transvaal specimens although the post-auricular patch is brighter.

Elephantulus edwardi

Macroscolides edwardii Smith, 1839. Oliphants River, Cape Province. (Probably the one flowing into the Atlantic, since it has subsequently been found in many parts of that district but not near the other Oliphants River in the Oudtshoorn district). Lectotype: B.M. (N.H.) 41.796, skin and skull (specimen labelled, but apparently never published, by Thomas).

Macroscolides edwardsii Sclater, 1901.

Elephantulus capensis Roberts, 1924. Klaver, Cape Province.

Elephantulus karoensis Roberts, 1938: 234. Deelfontein, north of Richmond, Cape Province.

Elephantulus rupestris: Ellerman *et al.*, 1953.

SPECIMENS EXAMINED. Southwestern Cape Province four (including one from the U.S. National Museum and one from the Kaffrarian Museum, King William's Town, both of these from Pakhuis Pass, Clanwilliam; and one from Klaver district, i.e. topotypical *capensis*); Little Namaqualand one (U.S. National Museum); central Cape Province seven (including topotypical *karoensis*); "S. Africa" five (including the type of *edwardi*).

TAXONOMIC STATUS. Roberts (1951) did not equate his *capensis* with *edwardi* because it did not appear to agree closely with Smith's description. But the type of *edwardi*, along with four specimens bearing this name received from Mr. Edward Verreaux (who collected the type material and after whom it was named) is in the British Museum. All these specimens agree closely with topotypes of *capensis* and of *karoensis*, which Roberts (1951) subsequently treated as a race of *capensis*. Ellerman *et al.* (1953) treated *edwardi* as conspecific with *E. myurus* (which they called *E. rupestris*). However, *edwardi* and *myurus* differ with respect to several apparently independent characters and a series of each is available from Deelfontein.

DESCRIPTION. See Table 1 for diagnostic characters and Text-figs. 7d, 8c, 9i and 10i for structural details. Head and body about 110–120 mm.; tail 130–140 mm.; hind feet about 32–35 mm.; ear about 25 mm. Dorsal pelage greyer than in the other southern species, tinged with yellow rather than with reddish brown, and more sharply separated from the grey flanks. The post-auricular region is tinged with yellowish brown, less conspicuously than in *E. rupestris* but more so than in southern *E. myurus* since there is a greater contrast with the greyish back. Ventral pelage grey. Tail black above, pale below at the base but completely black distally. Hairs very short at the base, increasing in length distally but not exceeding about 4 mm., i.e. considerably less tufted than that of *E. rupestris*.

Externally *E. edwardi* very closely resembles *E. rupestris* and *E. myurus*. From *E. rupestris* it can be distinguished by the darker ventral pelage, by the yellow rather than orange-buff behind the ears and by the shorter, less hairy tail. From *E. myurus* it can be distinguished less easily by the dark, slightly more tufted tail and the larger, more truncate, supratragus.

Skulls of *E. edwardi* can be readily distinguished from those of *E. rupestris* by the inflated ectotympanic and less inflated entotympanic bullae, and from both *E. rupestris* and *E. myurus* by the reduction of all but one principal cusp on P¹, the absence of any lingual cusps on P², the single-rooted P₁, and the non-sinuuous vertical suture between premaxilla and maxilla. In the region of overlap it can also be distinguished from *E. myurus* by its small size (Text-fig. 15). (One skull,

from Clanwilliam, has what appears to be a small lingual cusp on P², but the teeth are heavily worn and this may be an effect of wear).

RANGE. See Text-fig. II. Apparently in at least two segments: western Cape Province from Little Namaqualand south to Tulbagh district; and in the Upper Karroo from Richmond district to the coast at Port Elizabeth (the latter may be an isolated locality). The habitat appears to be the same as for the other southern species, i.e. rocky outcrops on grassland.

E. edwardi is marginally sympatric with *E. rupestris* in the north, with *E. myurus* in the northeast, and is more extensively sympatric with *Macroscelides proboscideus*.

REGIONAL VARIATION. The four dry specimens examined from the western part of the range differ slightly from the series from Deelfontein and one from near Graaf Reinet in the darker, more shortly haired tail (completely black above) and the purer grey flanks. The type of *edwardi* has a similarly dark tail, and the pelage appears to resemble the western rather than the eastern form, although its age makes such a comparison of doubtful validity. There is also a difference in size, the western sample, and the type of *edwardi*, being larger (Text-fig. 15). If these differences prove to be constant, the western form may be taken as the typical race (synonym *capensis*) and the eastern one as *E. e. karoensis*.

Elephantulus brachyrhynchus

Macroscelides brachyrhynchus Smith, 1836: 42. Between Kuruman (northern Cape Province) and the tropic in Bechuanaland. Lectotype (selected here from two syntypes): B.M. (N.H.) 39.10.5.5, skin labelled "S. Africa, Dr. Smith", associated with skull no. 59.5.7.17.

Macroscelides brevirostris Schintz, 1844: 284.

Macroscelides fuscus Peters, 1852. Boror, near Quelimane, Mozambique.

Macroscelides brachyrhynchus Bocage, 1882. Caconda, southeast of Benguela, Angola.

Macroscelides brachyrhynchus malosae Thomas, 1898. Mount Molosa, 5,500 ft., Malawi.

Macroscelides delamerei Thomas, 1901b: 155. Athi R., Kenya.

Nasilio brachyrhynchus albiventer Osgood, 1910. Lake Elmenteita, Kenya.

Nasilio brachyrhynchus luluuae Matschie, 1926. Near Luluaburg, Congo.

Nasilio brachyrhyncha tzaneensis Roberts, 1929: 85. Tzaneen, East Transvaal.

Nasilio brachyrhyncha langi Roberts, 1929: 85. Mazambo, lower Limpopo River, Mozambique.

Nasilio brachyrhyncha shortridgei Roberts, 1929: 86, Ndola, Zambia.

Nasilio brachyrhynchus mababiensis Roberts, 1932: 18. Tsotsoroga Pan, Ngamiland, Botswana.

Nasilio brachyrhyncha selindensis Roberts, 1937. Mount Selinda, Melsetter dist., Rhodesia.

SPECIMENS EXAMINED. The type and a paratype; Transvaal seven; South West Africa fourteen; Angola seventeen; Rhodesia fifteen; Zambia fifty-four, including strictly topotypical *shortridgei*; Mozambique eleven (including eight from the U.S. National Museum); Malawi seventeen (including the type of *malosae*); Congo twenty-one; Tanzania three (including one in the museum of the College of Wildlife Management, Mweka, Tanzania); Kenya thirty-two (including the type of *delamerei* and including twenty-three in the National Museum, Nairobi); Uganda three.

TAXONOMIC STATUS. Clearly defined from all other species except *E. fuscipes*. This species includes all forms that have hitherto been placed in the genus *Nasilio*

except *fuscipes*, which is considered a distinct species, and *schinzi*, which is believed to belong to *E. intufi*. Noack (1889) described *Macroscolides brachyrhynchus schinzi* on the basis of a single skin from "Ondongastamm, Ovamboland". The type was said by Shortridge (1934) to be in the Senckenberg Museum, Frankfurt, but it is no longer there. Several features of Noack's description point to *E. intufi*, rather than *E. brachyrhynchus*: pelage 15 mm. long, thick and fine; dorsal colour "ein lebhaftes bräunlich gemischtes Gelbroth"; tail well-haired, obscuring scales, yellow-grey above, lighter below, hairs black-tipped towards the end but no brush. *E. intufi* has subsequently been found in this area, but not *E. brachyrhynchus*.

DESCRIPTION. See Table 1 for diagnostic characters and Text-figs. 8d, 8e, 9b and 10b for structural details. Head and body variable, most often about 110–120 mm.; tail variable but usually shorter than head and body, 65 to 105%; hind feet usually 25–32 mm.; ear usually about 19 to 22 mm.

Dorsal pelage reddish or yellowish brown, about 10 mm. long, with emergent dark-tipped guard hairs, rather similar to some forms of *E. rufescens*. White eye-ring fairly prominent. Ventral pelage white-tipped but the white not quite obscuring the grey bases. Tail bicoloured, very shortly haired, the hairs uniform in length throughout.

E. brachyrhynchus is superficially most similar to *E. fuscipes*, *E. rufescens* and *E. intufi*. From *E. fuscipes* it can be distinguished by the absence of a pectoral gland and by the untwisted supratragus; from *E. rufescens* by the absence of a pectoral gland, absence of a post-ocular mark and shorter tail; and from *E. intufi* by the shorter, uniformly haired tail, and shorter hind feet (usually under 31 mm.). From *E. myurus* in the Transvaal it is readily distinguished by the predominantly brown rather than grey pelage and the short tail.

The adult skull can be distinguished from all but *E. fuscipes* by the presence of small, third lower molars. The cranial differences between it and *E. fuscipes* are discussed under that species.

RANGE. See Text-fig. 16. Steppe and savanna woodland zones from Transvaal, northern Botswana and northeastern South West Africa north to Kasai in the Congo and through Tanzania to Kenya and Uganda. In Tanzania comparison with the data available for other species suggests that it is genuinely absent from large areas, e.g. in the north.

E. brachyrhynchus is sympatric with *E. intufi* and *E. myurus* in the south and with *E. rufescens* in Kenya, but it is probable that it occurs in more wooded areas than these species (including riverside scrub in otherwise dry country). It overlaps more extensively with *Petrodromus tetradactylus* in Zambia, Malawi, Mozambique and the southern Congo. Records from Uganda are too few to show its geographical relationship with *E. fuscipes*.

REGIONAL VARIATION. See Text-fig. 17. Colour of pelage, relative length of tail and overall size show some regional variation. Wherever material is available from a number of scattered localities there are indications of clinal variation. It is possible that the major rivers may introduce some genuinely discontinuous variation, but in no case are sufficient specimens available from either side of a river to demon-

strate this. It is probable that more complete collections will in time render most, if not all, subspecific names invalid.

The collection from Zambia (including topotypical *shortridgei*) can be taken as a base for reference, since they are centrally placed in the range and are numerous enough to demonstrate the extent of individual and seasonal variation. Most of

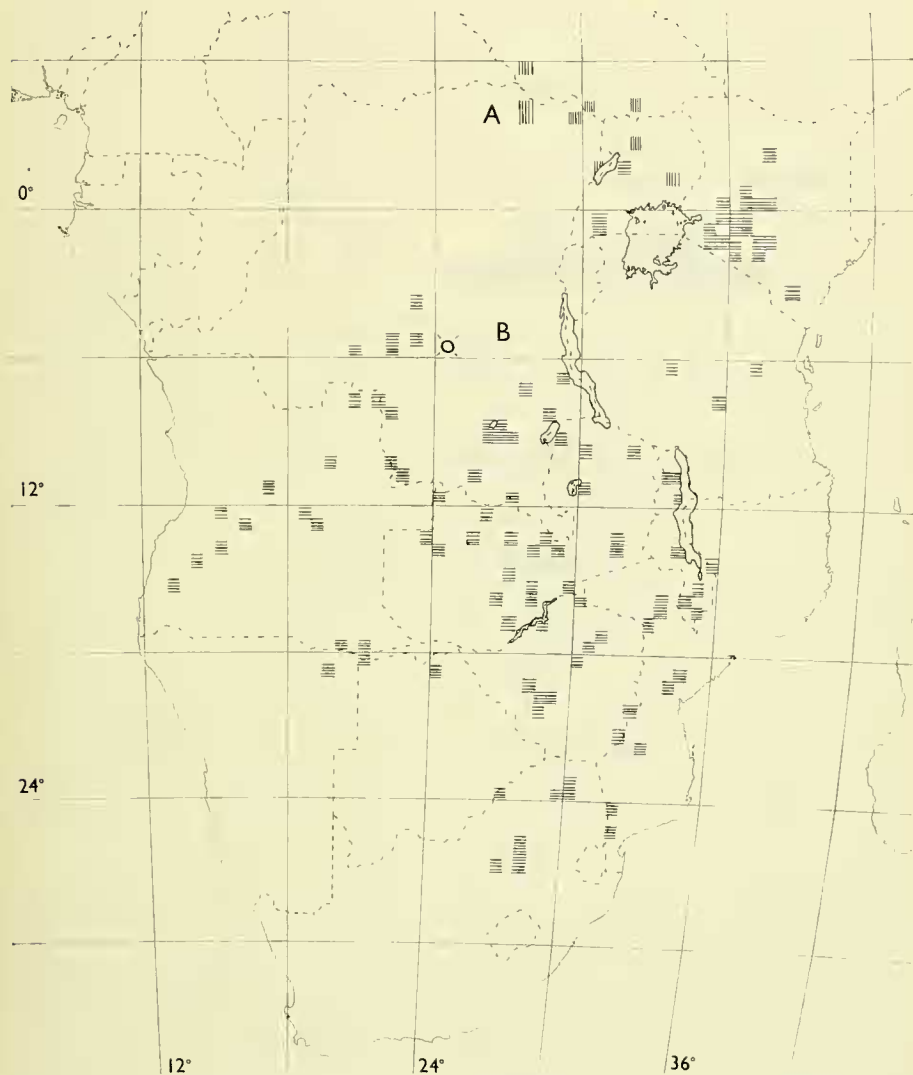


FIG. 16. The recorded distribution of A: *Elephantulus fuscipes*; B: *E. brachyrhynchus*
Circle: locality uncertain.

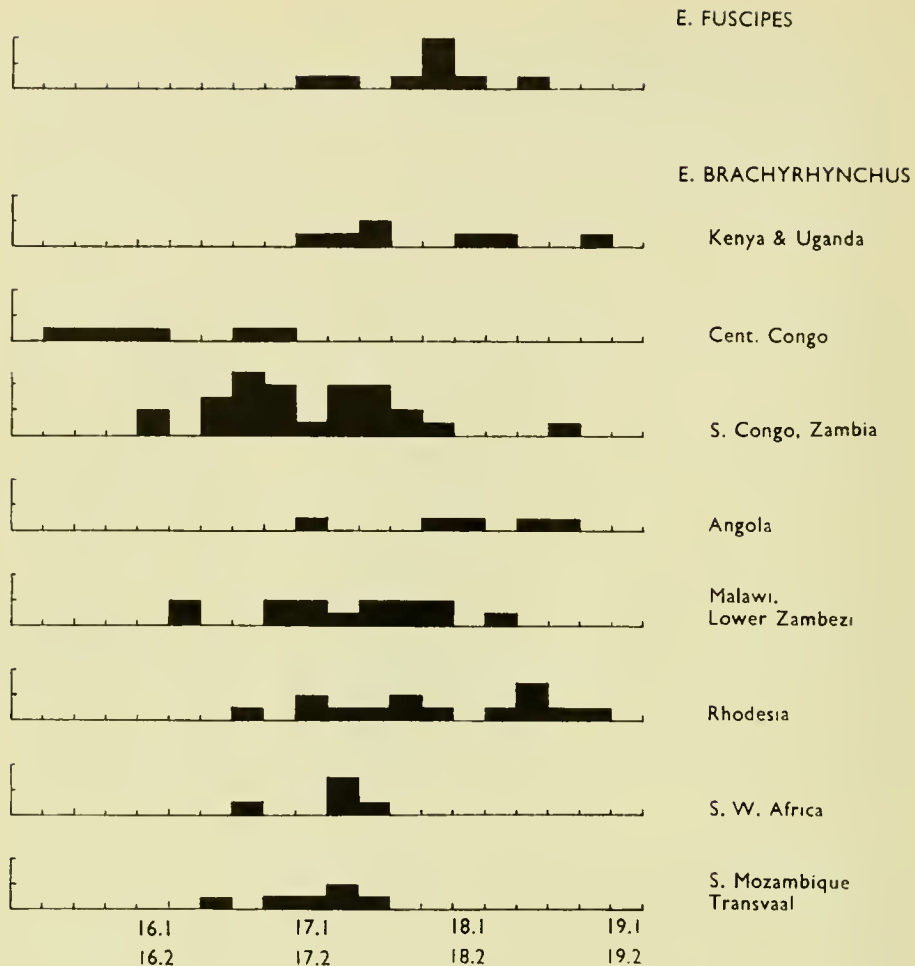


FIG. 17. Variation in length of upper tooth-row of *Elephantulus fuscipes* and *E. brachyrhynchus*.

the specimens were collected in the dry season and are distinctly yellowish brown above with much clearer buff on the flanks, the buff being demarcated rather sharply from the white ventral pelage. They are of medium size for the species (upper tooth-row 16.1–18.0) and the tail is of medium length (70–90% of head and body). Only two wet-season skins are available (from Solwezi) and they are distinctly darker. Five skins from Mwinilunga (extreme northwest) are more rufous than typical *shortridgei* from Ndola.

From Malawi the six available skins of *malosae* including the type, from high

altitude in southern Malawi, July to December, are dark greyish brown with very little yellow on the flanks. They are therefore very distinct from specimens from Zambia, but others from low altitude in southern Malawi are much less grey suggesting that there is no discontinuity between the two extremes. Skins from northern Malawi are very similar to those from Zambia but are slightly more rufous.

From Rhodesia eleven skins are available. All are similar to the two wet-season skins from Zambia although five were taken in the wet season (November and December: Essexvale) and the other six in the dry season (July to September: Mazoe, 1,200 m.). No topotypical material of *selindensis* (Melsetter district) has been seen, but this form was described mainly on the basis of its large size. In fact it does not differ in size from the available material from elsewhere in Rhodesia; there is wide overlap between these and Zambian specimens and therefore it is unlikely that *selindensis* has any validity. The relative tail-length in Rhodesia is high, about 85–105% of head and body.

From Transvaal six skins have been examined (July to September, Zoutpansberg, i.e. nearly topotypical *tzaneensis*). They are rather grey but very similar to those from Rhodesia. They are smaller than the two *tzaneensis* listed by Roberts (1951) (upper tooth-row 16.9–17.6). The tail is 88–96% of head and body. Roberts diagnosed *tzaneensis* by its large size (upper tooth-row 18.3 and 18.5) and darker dorsal pelage, compared with specimens from western Transvaal which he called *N. b. brachyrhynchus*, although the type locality of *brachyrhynchus* is indeterminate, between Kuruman in northern Cape Province and the tropic in Botswana. No material is available from Botswana nor Cape Province except the two cotypes which cannot be used for comparison of colour since they have been in spirit and exposed to light.

From South West Africa a series of fourteen is available from the extreme north-east (April to July). They show little variation in colour, being a very pale buffy grey, lacking the darker brown tones of Zambian skins. The white eye-ring is large and unbroken (the last feature being unique in the species). These are called *N. b. schinzi* by Shortridge (1934), but this name is applicable to *E. intufi*, not *E. brachyrhynchus* (see under "Taxonomic status" above).

From Angola, specimens are available from several localities indicating a transition from the grey montane form in the west (*brachyurus*) to the Zambian form already described. Three January skins from Fort Quilenges (14° 14' E.) are grey with a slight tinge of olive dorsally. Four topotypical *brachyurus* (Caconda, 15° 13' E., 1,740 m., September to December) are also very grey but lack the olive tinge. They are in fact very similar to the series from South West Africa but are darker. Two skins from Mount Moko (15° 18' E., 1,800 m., March) are similar but a little browner. Four from Munhango (18° 42' E., 1,300 m.) are much browner, but are still not so lacking in grey as dry-season Zambian skins. A further four from Lunda (19° 14' E., July to August) are similar.

In the Congo, skins from Katanga (two February, two July) are identical with corresponding skins from Zambia, showing the same seasonal difference. From Kasai a series of fourteen (June to November, topotypical of *luluae*) are darker and more rufous than Zambian ones and they are also small (upper tooth-row 15.6–

17.0, mean of six 16.2), and short-tailed (65–83% of head and body) although both of these measurements show a wide overlap with series from Katanga and Zambia. The contrast in colour between the samples from Kasai and from Katanga is paralleled (in a more extreme degree) in *Petrodromus tetradactylus* in which there is also an absence of material from the intervening region.

Specimens from Kenya and Uganda (referable to *delamerei*) are again greyer than those from Zambia, being only slightly less dark than *malosae* of southern Malawi, and scarcely distinguishable from *brachyurus* of western Angola. In spite of their apparent isolation from the southern forms it seems impossible to apply a sub-specific name, since no diagnosis can be made that excludes the greyer forms from southern Africa. Within East Africa variation is very slight.

ABNORMAL VARIATION. Of 102 adult skulls examined three have a small, unicuspid third upper molar on one side of the mouth (two from Zambia, one from Mozambique). Two wet-preserved animals (from Malawi and Mozambique) have the supratragus twisted backwards on a slightly constricted stalk, resembling that of *E. fuscipes* although less extreme (Text-fig. 8e). This condition appears to be present also in a dry skin from the lower Zambezi, and is clearly shown in the original figure of *fuscus* (Peters, 1852: pl. 19b). Tail-length also seems to be very variable in this region, and the situation clearly requires further investigation.

Elephantulus fuscipes

Macroselides fuscipes Thomas, 1894: 68. N'doruma, Niam-Niam country, North East Congo. Holotype: B.M. (N.H.) 84.5.1.6, in phenoxytol with skull extracted, juv. ♀.

SPECIMENS EXAMINED. Congo eight (including the type, and six borrowed from the Musée Royal de l'Afrique Centrale, Tervuren); Sudan one; Uganda five.

TAXONOMIC STATUS. Closely similar to *E. brachyrhynchus* with which it probably forms an allopatric pair.

DESCRIPTION. See Table 1 for diagnostic characters and Text-figs. 8f, 9c and 10c for structural details. No reliable external measurements are available but the following estimate can be made from dry skins: head and body about 120 mm.; tail 80–90 mm., always considerably shorter than the head and body; hind foot c. 25 mm. Specimens from Uganda appear rather larger than *E. brachyrhynchus* from Uganda.

Dorsal pelage dark brown, less red than most skins of *E. brachyrhynchus*. Ventral pelage with white tips which do not completely obscure the grey bases. Tail bicoloured, almost black above.

E. fuscipes is very similar to *E. brachyrhynchus* but can be distinguished externally from that species by the presence of a pectoral gland, by the peculiar, twisted supratragus, by the darker dorsal surface of the tail and by the absence of an interdigital pad at the base of the hallux. When not apparent, the pectoral gland can be detected by parting the hair transversely across the chest, when the hairs in the mid-ventral line will be seen to be short and white, contrasting with the long slaty bases of the adjacent hairs. The difference in the supratragus holds for all the

specimens of *E. brachyrhynchus* examined from Uganda and Kenya but several specimens from Malawi and Mozambique have the supratragus approaching the condition characteristic of *E. fuscipes*.

The skull of *E. fuscipes* is very similar to that of *E. brachyrhynchus*, being narrower than in most other species. The most nearly constant difference appears to be the greater spacing of the anterior teeth in *E. fuscipes*. In particular the gap between I³ and C¹ is longer than the alveolar length of C¹ in all the skulls of *E. fuscipes* examined. In *E. brachyrhynchus* the gap is shorter than C¹ in all but two East African skulls, the two exceptions being from the Laikipia Plateau, Kenya.

RANGE. See Text-fig. 16. Savanna of the extreme southwestern Sudan, north-eastern Congo and parts of Uganda. It is not known to be precisely sympatric with either *E. brachyrhynchus* or *E. rufescens*, but it is likely to be in some form of contact with these species.

DISCUSSION

Gross distribution

The distribution of the family and of the genera is shown in Text-fig. 18. The family as a whole is unique amongst exclusively African taxa of mammals in its absence from the whole of West Africa north and west of the Congo and Ubangi Rivers, in spite of its presence in the Atlas region. Although it is a distinct species, the northwestern *E. rozeti* is sufficiently similar to the other members of the genus *Elephantulus* to preclude the view that its isolation is very ancient. It therefore seems probable that this genus has become extinct in an intervening region in relatively recent times, e.g. during or since the Pleistocene. If Horst (1946) is correct in identifying the representations of the ancient Egyptian god Set as an elephant-shrew, which seems reasonable, this would suggest the Nile Valley as the link between the two segments of the range. It may be, therefore, that the family has never been present in the west African savanna in recent geological time, but there does not appear to be any other group of insectivorous mammals replacing the elephant-shrews in that region.

Ecological relationships of the species

In discussing this topic it will be convenient to reserve the word *sympatric* for gross overlap of the ranges of two species and to employ the term *syntopic*, as used by Rivas (1964), to denote species that "occur together in the same locality, are observably in close proximity, and could possibly interbreed". However, it seems that a further division of this concept is necessary to distinguish between species that occupy *different* habitats, meeting only on the boundaries of the habitats, and which we shall call *marginally syntopic*; and species that occupy the *same* habitat so that most individuals are liable to meet members of the other species, and which we shall call *widely syntopic* species. In fact it is probably very rare in mammals to find a pair of congeneric species that are sympatric without being at least marginally syntopic, but by using the word syntopic for such intimate contact, the terms *marginally sympatric* and *widely sympatric* can be used to denote the extent of gross overlap of the ranges.



FIG. 18. Distribution of the genera of Macroscelididae.

It is rare for more than two species of elephant-shrew to be syntopic in either sense. The species of *Rhynchocyon*, themselves allopatric, are confined to forest or very thick bush with a closed canopy. They come into contact chiefly with *Petrodromus tetradactylus*, which extends also into the denser savanna woodlands. The latter has been seen within a few yards of *R. petersi* in the Shimba Hills in Kenya. *Rhynchocyon cirnei* might be expected to have marginal contact also with *E. fuscipes* in the northeastern region of the Congo, and in Uganda; and with *E. brachyrhynchus* in Malawi and southeastern Congo. *P. tetradactylus* is widely sympatric with *E.*

brachyrhynchus, e.g. throughout Zambia. In the Luangwa Valley *P. tetradactylus* has been observed in mopane woodland adjacent to areas of tall grass in which *E. brachyrhynchus* was trapped. A similar situation may obtain in southern Tanzania but records of *E. brachyrhynchus* in Tanzania are peculiarly scarce. *E. rufescens* also abuts with *P. tetradactylus* in Tanzania but since the former is especially characteristic of the short-grass plains any overlap is likely to be slight.

E. rufescens and *E. brachyrhynchus* are sympatric in the Central Highlands of Kenya but they are probably only marginally syntopic. None of the available records are sufficiently precise to throw light on the ecological relationship of the two species. Elsewhere in East Africa any overlap of species is only marginal, e.g. between *E. rufescens* and *E. revoili* in Somalia and perhaps between *E. brachyrhynchus* and *E. fuscipes* in Uganda.

South of the Zambezi sympatry of two or more species is more frequent, although good evidence of syntopy is scarce. *E. brachyrhynchus* overlaps extensively with *E. intufi* and *E. myurus* but these latter form an east-west pair only marginally in contact. Further south, *E. intufi* overlaps very extensively with *E. rupestris* in South West Africa, but they are probably only marginally syntopic since Shortridge (1934) did not find them in precisely the same locality. Further south yet, both *E. rupestris* and *E. myurus* are replaced by *E. edwardi*. A report by Shortridge (1942) suggests that *E. rupestris* and *E. edwardi* are syntopic in rocky habitats in Little Namaqualand. All three of these species approach each other closely at Deelfontein in Cape Province but there is no information on habitats in that area.

M. proboscideus is widely sympatric with both *E. rupestris* and *E. edwardi* and at least comes close to *E. myurus* at Deelfontein. According to Shortridge (1934) it is widely syntopic with *E. rupestris* in parts of South West Africa where they "often occur side by side in about equal numbers, the two species being indistinguishable from a distance".

There is therefore no good evidence of even two species of *Elephantulus* being widely syntopic over any large area and in most cases of gross sympatry the species are likely to be separated by habitat preference rather than by differential exploitation of the same habitat. By contrast *M. proboscideus* seems likely to be widely syntopic with *E. rupestris* and in this connection it would be interesting to have details of food especially in view of the much greater degree of hypsodonty in *M. proboscideus*.

Uncertainties

Taxonomic uncertainty at the specific level concerns chiefly two situations. In *Rhynchocyon* there may be found grounds for treating the form *stuhlmanni* as specifically distinct from *R. cirnei*. In *Petrodromus* the same may be said for the form *tordayi* in the Congo in relation to *P. tetradactylus*. However, in the case of *Petrodromus* there is less certainty that the two forms are spatially isolated than in the case of *Rhynchocyon*. Further areas requiring investigation of *Petrodromus* are northeastern Tanzania where the complex interaction of *P. t. sultan* and *P. t. rovumae* would repay study; and in southern Mozambique to determine the spatial and morphological relationship of *P. t. schwanni* to the adjacent forms.

Within the genus *Elephantulus* a question of particular interest is the nature of the relationship between the members of the two species-pairs, namely *E. brachyrhynchus*/*E. fuscipes* in Uganda, and *E. rufescens*/*E. revoili* in Somalia. Any case of syntopy would repay study, but an area of especial interest would seem to be the Richmond district of Cape Province where three species of *Elephantulus* and *Macroscelides proboscideus* all approach each other closely. Specimens of all four species from Deelfontein are in the British Museum (collected in 1901 and 1902). That these did indeed come from a limited area is suggested by the fact that both *E. myurus* and *E. rupestris* were collected on one day; and *E. myurus* and *E. edwardi* on one day with *M. proboscideus* the previous day.

The subspecific taxonomy can only be clarified by a great deal of further collecting to determine especially the detailed range of each species. Areas from which data is especially scanty are Angola, Mozambique and Somalia.

NEW NAMES

The name *Rhynchocyon cirnei shirensis* subsp. n. is proposed (p. 59), type locality Lichenja Plateau, Mlanje Mountain, Malawi.

The name *Elephantulus broomi* nom. nov. is proposed (p. 54) to replace *E. langi* (Broom, 1937), preoccupied by *langi* Roberts, 1929.

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